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Habitat and Demography of Understory Trees in Mixed Species Hardwood Forests in Northern Florida, United States of America.

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HABITAT AND DEMOGRAPHY OF UNDERSTORY TREES IN MIXED SPECIES HARDWOOD FORESTS IN NORTHERN FLORIDA, USA

A Dissertation

Submitted to the Graduate Faculty of the
Louisiana State University and
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In

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ABSTRACT

Temperate mixed-species hardwood forests of northern Florida, USA, contain a high diversity of understory tree species, some of which have been hypothesized to require disturbance (e.g., hurricanes and/or treefall gaps). *Taxus floridana* is a rare understory conifer endemic to midslopes of ravines of the Apalachicola River Bluffs, and is found primarily on north-facing slopes. Vegetation sampling in the southern portion of *T. floridana*'s range revealed the presence of an upslope oak-hickory community of suggested recent origin, and higher densities of American beech (*Fagus grandifolia*), southern magnolia (*Magnolia grandiflora*), and evergreen understory trees on north-facing midslopes with *T. floridana* than on randomly chosen north-facing midslopes. Thus, *T. floridana* presently exhibits high habitat specificity to restricted areas of north-facing midslopes. The status of *T. floridana* was investigated by acquiring demographic data on stem recruitment, survival, and growth, in three different populations (Rock Creek, Long Branch, and Beaverdam Creek) over four years. Seedling recruitment was temporally variable; seedling recruitment was also characterized by an episode in 1996 that was approximately ten-fold higher than in the proceeding years. Fates of seedlings varied both spatially and temporally, while fates of non-seedling stems with small diameters varied spatially. Growth of individual stems was similar in all populations sampled. Periodic matrix models incorporating such demographic data predicted declining growth rates for all sampled populations of *T. floridana*. This is consistent with recent anthropogenic changes in *T. floridana*'s habitat, and/or its

prolonged existence in low quality habitats. Annual episodic regeneration essentially did not influence population growth rates. Increasing the survival of juvenile stems may help promote net positive population growth in such rare species. Finally, recruitment of *Ostrya virginiana* and *Carpinus caroliniana*, two more common understory species was examined following Hurricane Kate in 1985 using long-term data from Woodyard Hammock in north Florida. Post-hurricane recruitment was equally high in gaps of different ages (i.e., different histories), and was higher than in areas under closed canopy. The presence of a juvenile sapling bank before and at the time of Kate may be responsible for their present dominance in the understory stratum in Woodyard Hammock.

GENERAL INTRODUCTION

Warm temperate mixed species hardwood forests of the southeastern Gulf coastal plain are among the most diverse closed canopy hardwood forests in the continental United States (Platt and Schwartz 1990, Quigley and Platt 1996). They contain a wide variety of deciduous and evergreen woody overstory and understory species, many of which have been present in North America since the Mesozoic and Cenozoic eras. The present physiognomy of these forests is quite similar from east Texas through northeastern Florida (see Marks and Harcombe 1975, 1981, Harcombe and Marks 1978, Glitzenstein et al. 1986, Platt and Schwartz 1990, Quigley and Platt 1996, Batista and Platt 1997). However, endemic tree species (e.g., *Torreya taxifolia* (Arn.) and *Taxus floridana* Nutt.) are only found in the Apalachicola River Bluffs region of northern Florida.

Mixed species hardwood forests in northern Florida, which are also called hammocks (Harper 1905), historically occur as disjunct bands of vegetation located between upland pinelands and bottomland hardwood or floodplain forests (Platt and Schwartz 1990, Schwartz 1994). Many of the present tree species are postulated to have been in these forests since the Miocene, since the southeastern coastal plain has been characterized by a relatively constant climate over the past 20,000 years (Delcourt and Delcourt 1984, 1987). In the Florida panhandle, southern migration of a subset of species took place during the Pleistocene when sea levels declined, while

northern migration of certain species occurred following the last post-glacial warming period.

The tree species composition of mixed species hardwood forests in northern Florida, as well as throughout the southeastern United States, has been characterized by location along the topographic gradient. Distinct species compositions have been noted in high, midslope, and low hammocks in both north Florida (Clewell 1986, Wolfe et al. 1988, Platt and Schwartz 1990) and elsewhere (Marks and Harcombe 1981). This gradient is readily observable in hardwood ravine forests of the Apalachicola River Bluffs, where elevational changes of greater than 30 m can occur quickly from creek bottoms to upland pinelands. These forests also contain *Taxus floridana*, an endemic, long-lived, slow-growing understory conifer confined primarily to north-facing midslopes. My first objective was to examine if the composition of overstory and understory trees in this region were a function of aspect, and whether north-facing slopes containing *T. floridana* were vegetationally distinct from north-facing slopes where *T. floridana* did not occur. This investigation was performed, in part, to examine the local rarity of *T. floridana*, and is the subject of Chapter 1.

Taxus floridana is a viable candidate for conservation studies for a number of reasons. It is a species with a small geographic range and narrow habitat specificity (i.e., characteristics of species rarity sensu Rabinowitz 1980, Rabinowitz *et al.* 1986) that has recruited few small stems over the past decade, but has also likely been present since the Miocene. Knowledge of current demographic trends may be useful to predict whether such rare,

potentially long-lived, slow-growing woody plants can continue to persist over long periods of time, or if plausible, unobserved demographic changes, which may be environmentally driven, might be necessary. Thus, my second primary objective was to describe the demography of *T. floridana* in populations throughout its range, and to predict whether long-term population growth will be likely by modeling its population dynamics. This analysis, which incorporated both spatial and temporal variation, is the subject of Chapter 2.

Treefall gaps are an important disturbance agent in warm temperate mixed species hardwood forests of northern Florida. Hurricanes occur frequently in these forests (on average more than once during the lifetime of adult trees) and can open a large portion of the canopy. This was documented in Woodyard Hammock in the Tallahassee Red Hills region of northern Florida following Hurricane Kate, which occurred in November of 1985 (Batista and Platt 1997). Such openings have been hypothesized to be critical for the persistence of understory trees (Peters and Platt 1996). However, following a hurricane, local areas within individual treefall gaps have their own prior history (e.g., time since gap formation); thus the demographic responses of understory trees in local areas in gaps following hurricanes may be quite variable. Thus, my final objective was to examine the importance of treefall gaps and the effects of prior gap history on the demography of understory species in Woodyard Hammock. This investigation was performed to examine if the dynamics of understory species was similar throughout Woodyard Hammock following Hurricane Kate, and is the subject of Chapter 3.

CHAPTER 1

THE DISTRIBUTION OF TREE SPECIES IN STEEPHEADS OF THE APALACHICOLA RIVER BLUFFS, FLORIDA[1]

INTRODUCTION

Warm temperate mixed species hardwood forests, which occur throughout the southeastern United States, rank among the most diverse closed-canopy hardwood forests in the continental United States (Platt and Schwartz 1990, Quigley and Platt 1996). Among these forests are unique steephead ravine forests that occur on sandy bluffs along the eastern tributaries of the Apalachicola River in the Florida panhandle (Sharp 1938, Means 1975). Overstory tree species abundances in these steephead forests change along steep slopes (Wolfe et al. 1988). Ridgetop sandhills are dominated by longleaf pine (*Pinus palustris* Mill.). Upper slope xeric hardwood forests are dominated by oaks (e.g., *Quercus hemisphaerica* Bartr. Ex Willd., *Q. geminata* Small) and hickories (e.g., *Carya glabra* [Mill.] Sweet, *C. tomentosa* [Poir. In Lam.] Nutt.). Midslope mesic hardwood forests are dominated by American beech (*Fagus grandifolia* Ehrh.) and southern magnolia (*Magnolia grandiflora* L.). Lower slope hydric hardwood swamp forests are dominated by bays (e.g., *Magnolia virginiana* L.) and gums (*Nyssa sylvatica* var. *biflora* [Walt.] Cory). Woody species composition along steephead slopes elsewhere in Florida also may be influenced by slope position, as well as slope angle and, to a lesser extent, soil nutrient properties (White and Judd 1985, Gibson 1992).

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Despite the general recognition of the importance of gradients in topography and soil moisture (e.g., Schwartz 1990), effects of slope position and azimuth on the distribution of tree species of the Apalachicola River Bluffs have not been assessed quantitatively. We addressed the question of the effect of position and aspect of slopes on densities of woody tree species along steephead slopes of the Apalachicola River Bluffs using data from randomly located north- and south-facing belt transects that spanned the elevation gradient within three steephead ravine systems.

Hardwood forests of steepheads of the Apalachicola River Bluffs are noted for endemic and disjunct populations of trees, understory shrubs, and herbs (Platt and Schwartz 1990). These species migrated southward following the most recent sea level decrease in the Pleistocene (see Neill 1957 for review of hydrogeology). One endemic species is the Florida yew, *Taxus floridana* Nutt., a 'rare' (sensu Rabinowitz 1981, Rabinowitz et al. 1986) understory shrub that occurs primarily along steephead midslopes (Wolfe et al. 1988). This species does not occur outside the Apalachicola River Bluffs region, despite floristically and ecologically similar areas in the immediate vicinity (Marianna Lowlands [see Mitchell 1963, Stalter and Dial 1986] and Tallahassee Red Hills [see Platt and Hermann 1986, Peters and Platt 1996, Quigley and Platt 1996]) and elsewhere in northern Florida (e.g., White and Judd 1985, Gibson 1992). Little is known of the factors limiting the historical or present-day distribution of *T. floridana*. Within steepheads of the Apalachicola River Bluffs, almost all populations of *T. floridana* are comprised mainly of large individuals in

scattered, subdivided populations located almost exclusively along north-facing slopes. Survival of these large individuals involves layering and sprouting (Redmond 1984). Although large *T. floridana* produce seeds, virtually no seedling recruitment of new individuals has occurred during the past decade (C. Kwit and W. J. Platt, personal observation).

In this study, we addressed the question of whether differences in tree species composition occurred along random north-facing slopes and north-facing slopes containing adult *T. floridana* individuals using belt transects. We also examined if endemic, subdivided species, such as *T. floridana*, occur primarily in some subset of north-facing slopes.

METHODS

Study Site

The Apalachicola River Bluffs of northern Liberty and Gadsden Counties (Florida, USA) are located on the east side of the Apalachicola River. Lateral seepage of ground water along the bluffs has resulted in formation of 3 to 5 km long ravine systems containing continuous, cool, spring-fed streams that flow perpendicular to the Apalachicola River (Means 1975). The Apalachicola River Bluffs are also bisected by the Pleistocene-aged Cody Scarp. North of this escarpment, there are gully-eroded ravines with sandy clay soils of Miocene age. South of the escarpment, there are steepheads with coarse wave-washed sands (Platt and Schwartz 1990). Our study was conducted within three steepheads (Beaverdam Creek, Little Sweetwater Creek, and Kelley Branch) of the Florida Nature Conservancy's Apalachicola Bluffs and Ravines Preserve

(Fig. 1.1). These ravine systems are surrounded by clearcut and fire-suppressed upland *Pinus palustris* sandhills presently under restoration (Seamon et al. 1989). Ravines within the preserve have experienced selective logging of hardwoods (Schwartz 1990).

Field Methods and Analyses

We sampled a total of 75 similarly sized 6 m wide belt transects that ran from bottom to top of ravines along Beaverdam Creek, Little Sweetwater Creek, and Kelley Branch. Nineteen transects, with azimuths between 270° and 90°, were randomly located on north-facing slopes (hereafter, random north-facing slopes). Thirty-one transects, with azimuths between 90° and 270°, were randomly located on south-facing slopes (hereafter, random south-facing slopes). None of these transects contained any *Taxus floridana* stems ≥ 2 cm diameter at 1.5 m height (hereafter, dbh). Twenty-five additional transects were located on north-facing slopes such that each contained at least one adult *T. floridana* stem ≥ 2 cm dbh (hereafter, *T. floridana* north-facing slopes). Within each 6 m wide transect, species (nomenclature throughout follows Godfrey [1988]), dbh, and distance from the bottom of the transect were recorded for each woody stem ≥ 2 cm dbh. A total of 6656 woody stems were sampled. Importance values were calculated by taking the average of density (individuals per 100 m^2) and basal area (cm^2 basal area per m^2) for each species over the entire area sampled, and converting the average for each species to a percentage (Whittaker 1975, White et al. 1990).

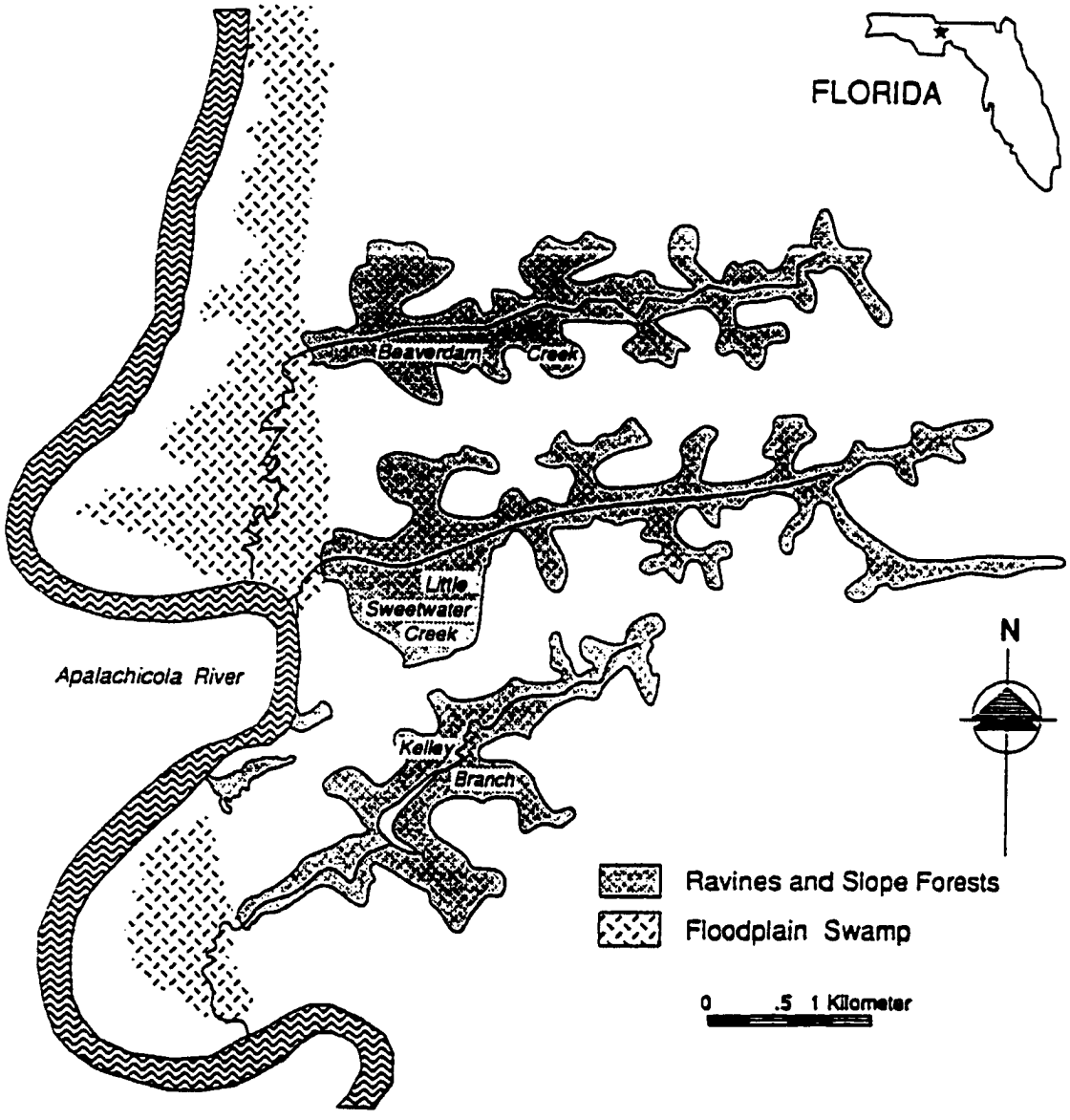

Figure 1.1. Three steephead ravines containing slope forests within the Apalachicola Bluffs and Ravines Preserve, located north of Bristol in Liberty County, Florida, USA. The steephead ravine systems (Beaverdam Creek, Little Sweetwater Creek, and Kelley Branch) all flow from upland longleaf pine savannas (white area) westward to the bluffs, where they flow down into floodplain swamp forests and empty into the Apalachicola River. Each ravine system contains spring-fed permanent streams that flow into the main creek channel.

For each woody stem, elevations relative to bottom of the creek were estimated using trigonometric calculations of slopes of transects along ravine inclines. Slopes were recorded at several arbitrary points located between slope changes along transects. All woody stems were first grouped into elevation classes of 1 m intervals, such that woody stems located from 0 to 0.99 m elevation were grouped into elevation class 1, 1.0 to 1.99 m in elevation in elevation class 2, etc. All stems located at or above 17 m were included in elevation class 18. Slope and distance measures were used to calculate the total area of ground sampled in each meter of elevation.

The 18 elevation classes were grouped into three slope positions (lower slope, midslope, and upper slope) that were subsequently applied to each transect. The grouping of elevation classes was accomplished by Minimum Variance Cluster Analysis (Ward 1963) using the CLUSTER procedure in SAS (SAS Institute 1989). Cluster analysis was applied to a matrix of densities (natural log [individuals per 10 m^2 + 1]) of 14 of the most important species pooled by elevation class (see Results).

The statistical design followed a completely randomized split-plot design, with slope type (random north-facing, random south-facing, and *T. floridana* north-facing) treated as a whole plot. Specific comparisons pertaining to the additional objectives of the study, the effects of aspect (i.e., random north-facing vs. random south-facing) and type of north-facing slope (i.e. random north-facing vs. *T. floridana* north-facing) on densities of important species, were stratified within slope type. Slope position (lower slope, midslope, and

upper slope) was treated as a subplot within whole plots. Our dependent variables of interest were densities of the most important species, which were natural log transformed (natural log [stems per 100 m^2 + 1]) to achieve normality. Multivariate Analysis of Variance (MANOVA) was employed using the GLM procedure in SAS (SAS Institute 1989). Variation among transects served as the error term for comparisons involving whole plots, and residual variation served as the error term for comparisons involving subplots. Overall effects of slope type, slope position, and their interaction were significant (Wilks' Lambda = 0.312, 0.037, and 0.362 respectively, each $P < 0.0001$). Thus, Tukey's Studentized Range tests were used to compare densities of species as a function of slope position, while Tukey-Kramer multiple comparisons of means were used to compare densities of species as a function of aspect, and type of north-facing slope.

RESULTS

General Overview and the Importance of Slope Position

The survey of 75 belt transects resulted in 14 species with importance values > 2.0 (Table 1.1). These species were abundant in most transects. *Pinus glabra* Walt. and major overstory species such as *Quercus hemisphaerica*, *Carya* spp., *Magnolia grandiflora*, *Qurecus alba* L., and *Fagus grandifolia* had high importance values. Four understory species (*Osmanthus americanus* [L.] A. Gray, *Kalmia latifolia* L., *Vaccinium arboreum* Marsh., and *Ilex opaca* Ait.) exhibited importance values similar to those of common overstory trees. However, as a result of smaller sizes, most understory

Table 1.1. Species, densities, basal areas, and importance values of species with importance values > 2.0. Data are based on counts from total area sampled in all 75 transects.

Species	Density (stems/100m^2)	Basal Area (cm^2/m^2)	Importance Value
OVERSTORY SPECIES			
Quercus hemisphaerica[a]	3.055	8.070	23.45
Carya spp.[b]	1.323	2.554	8.17
Fagus grandifolia	0.447	2.605	6.43
Magnolia grandiflora	0.419	2.153	5.42
Quercus alba	0.598	1.609	4.65
Pinus glabra	0.257	0.923	2.49
UNDERSTORY SPECIES			
Osmanthus americanus	3.315	0.932	8.95
Kalmia latifolia	2.115	0.352	5.20
Vaccinium arboreum	1.932	0.306	4.72
Ilex opaca	1.003	0.855	3.92
Ostrya virginiana	0.978	0.527	3.17
Oxydendrum arboreum	0.725	0.750	3.11
Illicium floridanum	1.112	0.071	2.49
Ilex coriacea	0.968	0.072	2.19

[a]includes some individuals of Quercus geminata

[b]groups together Carya glabra and Carya tomentosa

species, including *Ostrya virginiana* (Mill.) K. Koch, *Oxydendrum arboreum* (L.) DC., *Illicium floridanum* Ellis, and *Ilex coriacea* (Pursh) Chapm., exhibited low importance values. The fourteen species were used in subsequent analyses.

Three slope positions (lower slope, midslope, and upper slope) were quantified by Minimum Variance Cluster Analysis. Lower slope elevation classes (1-3), midslope elevation classes (4-12), and upper slope elevation classes (13-18) were grouped together as most similar with respect to densities of the 14 most important species (clusters with semi-partial $r^2 > 0.1$; Fig. 1.2). This delineation of slope positions most likely resulted from important species being significantly associated with a particular slope position or combination of contiguous slope positions (Tukey's Studentized Range Test, $P < 0.05$; Fig. 1.3). The density of *Ilex coriacea* and *Illicium floridanum* was roughly four times higher along lower slopes than mid or upper slopes; the density of *K. latifolia* and *Oxydendrum arboreum* along lower and midslopes was approximately twice that along upper slopes. *Fagus grandifolia*, *Ilex opaca*, and *M. grandiflora* attained peak density along midslopes, averaging twice that found along lower and upper slopes. The density of *P. glabra*, *Osmanthus americanus*, and *Q. alba* was approximately two to four times higher along midslopes and upper slopes than lower slopes. *Carya* spp., *Ostrya virginiana*, *Q. hemisphaerica*, and *V. arboreum* exhibited densities that ranged from twice to over four times higher along upper slopes than mid- or lower slopes. The clustering of lower slope, midslope, and upper slope elevation classes greatly reduced the complexity of the subsequent analyses.

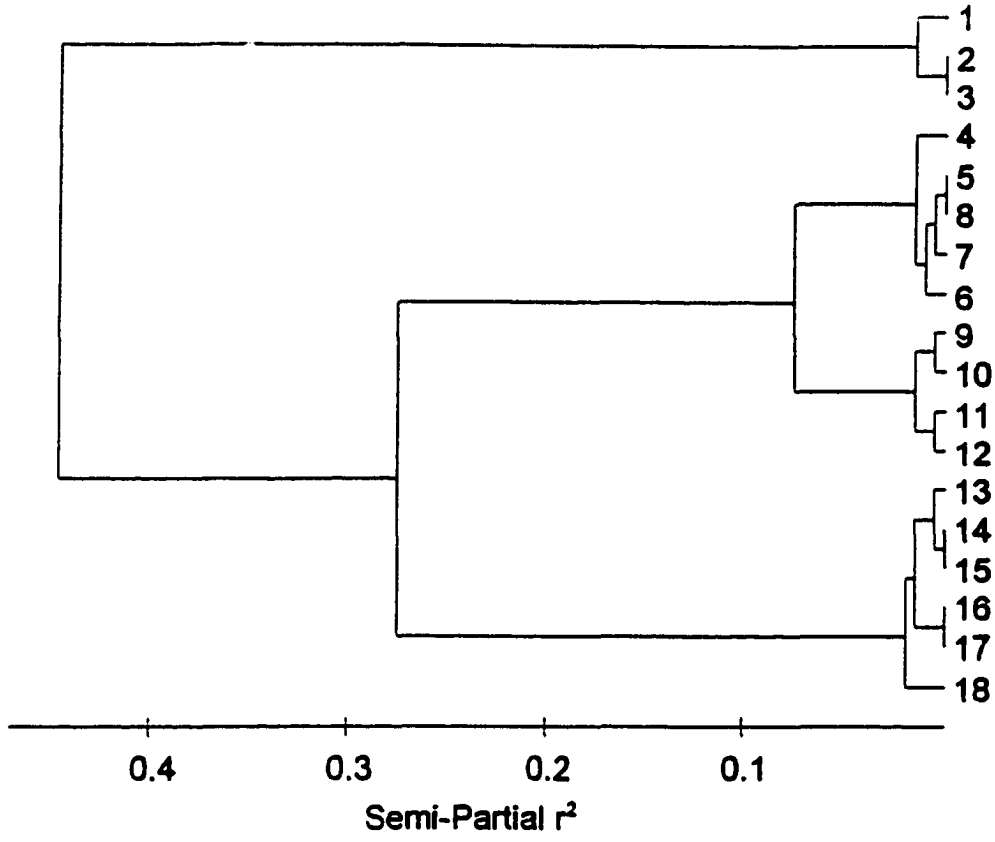

Figure 1.2. Dendrogram from Minimum Variance Cluster Analysis applied to a matrix of important species densities (natural log [stems/10 m^2 + 1]) pooled by elevation class (representing meters in elevation relative to the creek at the bottom of each transect). Lower, mid-, and upper slope positions appear as distinct vegetation types with a cut level of 3.

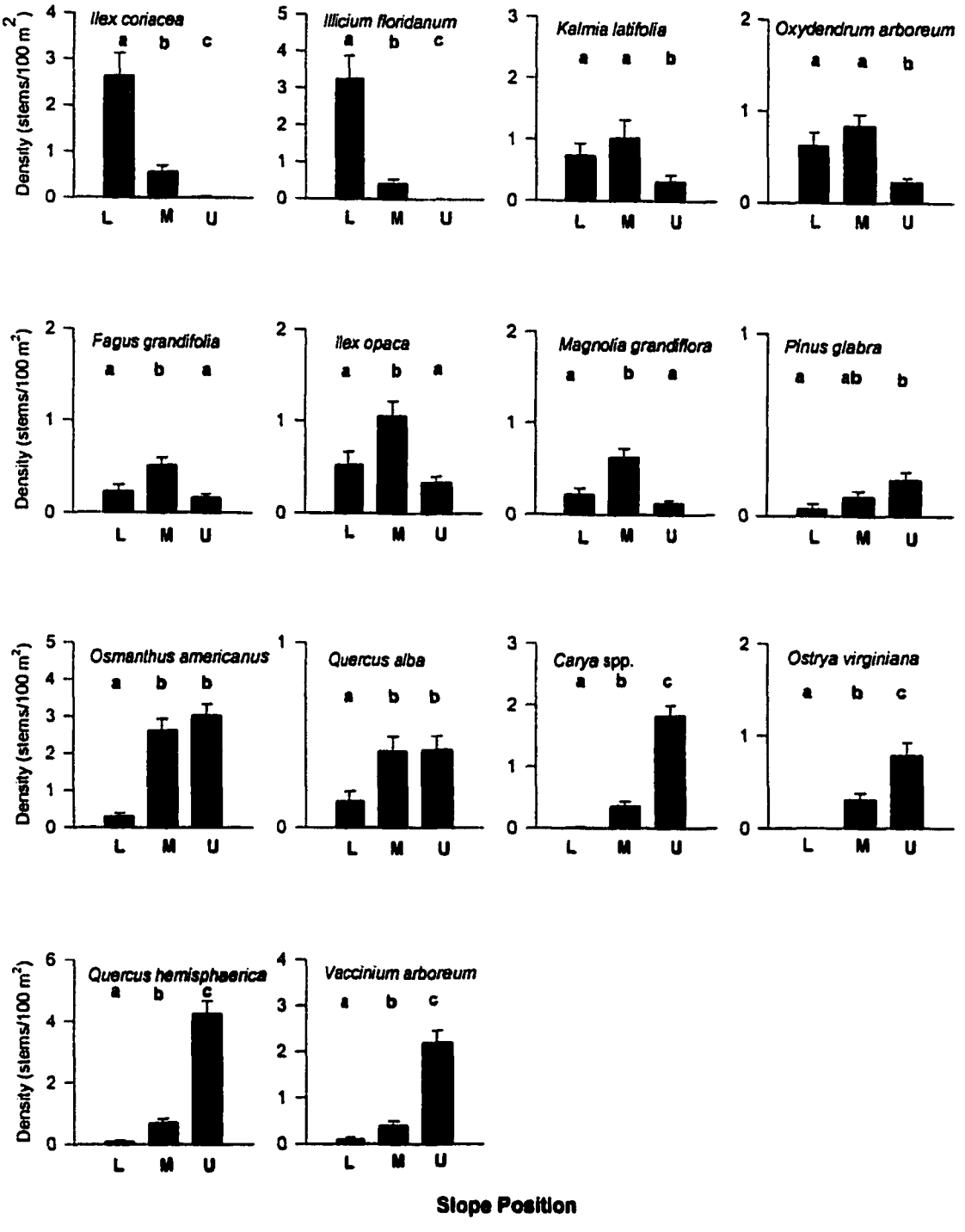

Figure 1.3. Densities (back-transformed ± Standard Error) of important woody species (stems ≥ 2 cm dbh) as a function of lower (L), mid- (M), and upper (U) slope positions of steepheads in the Apalachicola River Bluffs region of northern Florida. Means with the same letter are not significantly different (Tukey's Studentized Range Test, $P > 0.05$).

The Importance of Aspect

Aspect, irrespective of slope position, had little effect on species densities. Only the densities of *Q. hemisphaerica* and *V. arboreum* were significantly higher along random north-facing slopes than random south-facing slopes (Tukey-Kramer multiple comparisons of means, $P < 0.05$). The density of *Q. hemisphaerica* was on average 1.25 times higher on random north-facing slopes than random south-facing slopes, and the density of *V. arboreum* was roughly twice as high on random north-facing slopes than along random south-facing slopes.

The effects of an interaction between aspect and slope position on stem density were significant only for *Q. hemisphaerica* and *V. arboreum* (Tukey-Kramer multiple comparisons of means, $P < 0.05$; Fig. 1.4). Densities of *Q. hemisphaerica* were approximately two times higher on random north-facing upper slopes than on random south-facing upper slopes, and densities of *V. arboreum* were roughly three times higher on random north-facing midslopes than on random south-facing midslopes.

The Importance of Type of North-Facing Slope (with and without *Taxus floridana*)

Densities of *Ilex coriacea*, *F. grandifolia*, *K. latifolia*, *M. grandiflora*, and *P. glabra* were significantly higher along *T. floridana* north-facing slopes than random north-facing slopes (Tukey-Kramer multiple comparisons of means, $P < 0.05$). Among species, differences in density ranged from two (*Ilex coriacea*) to over fifteen (*K. latifolia*) times higher along *T. floridana* north-facing slopes. The

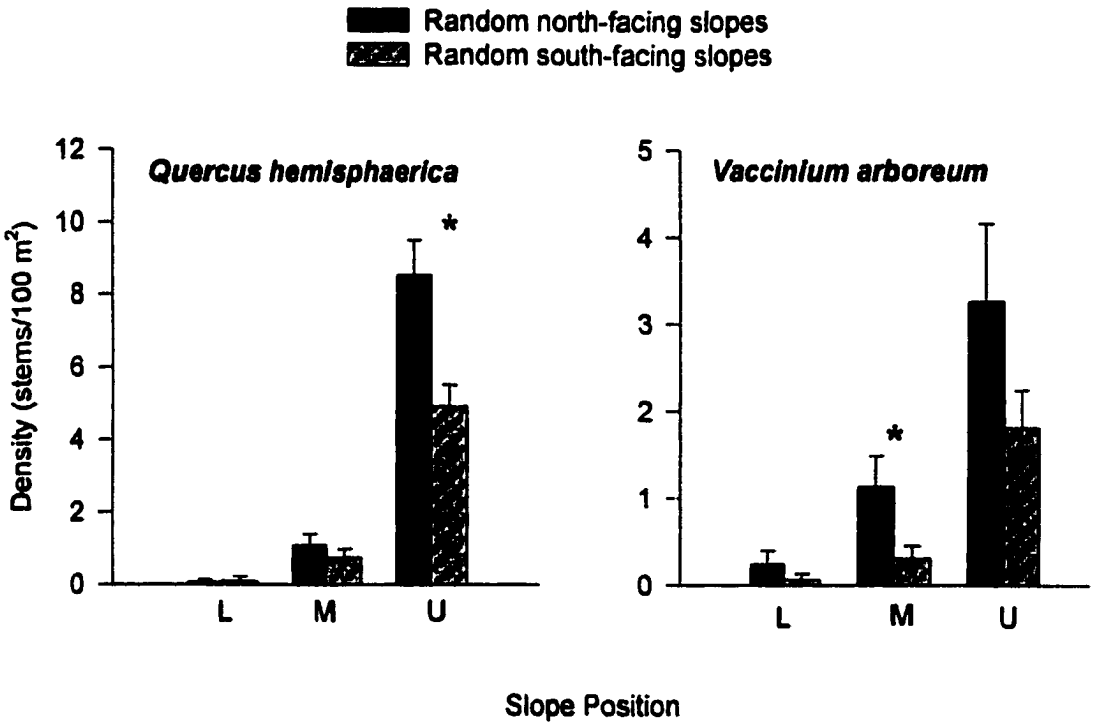

Figure 1.4. Densities (back-transformed ± Standard Error) of *Quercus hemisphaerica* and *Vaccinium arboreum* (stems ≥ 2 cm dbh) as a function of aspect and slope position (L = Lower Slope, M = Midslope, U = Upper Slope). Asterisks denote significant differences at particular slope positions (Tukey-Kramer multiple comparison of means, $P < 0.05$).

density of *Q. hemisphaerica* and *V. arboreum*, however, was significantly higher along random north-facing slopes than *T. floridana* north-facing slopes (Tukey-Kramer multiple comparison of means, $P < 0.05$), with densities approximately 2.5 times higher along random north-facing slopes.

The interaction of type of north-facing slope and slope position on stem density was evident for a number of species (Tukey-Kramer multiple comparisons of means, $P < 0.05$; Fig. 1.5). The density of *F. grandifolia* and *Ilex coriacea* was two to three times higher along *T. floridana* north-facing midslopes than along random north-facing midslopes. Although not statistically significant, this pattern was also observed for *Ilex opaca* and *M. grandiflora*. In contrast, the densities of *Carya* spp., *Osmanthus americanus*, *Q. hemisphaerica*, and *V. arboreum*, species typically associated with upper slopes, were two to five times lower along *T. floridana* north-facing midslopes than random north-facing midslopes (each $P < 0.05$, except *Q. hemisphaerica* with $P < 0.1$). The density of *Ostrya virginiana* and *P. glabra* was three to four times higher along *T. floridana* north-facing upper slopes than random north-facing upper slopes. The density of *Q. hemisphaerica* was over three times lower along *T. floridana* north-facing upper slopes than random north-facing upper slopes. *Kalmia latifolia* densities were notably higher at all slope positions on *T. floridana* north-facing slopes than random north-facing slopes.

Discussion

The abundance of woody species in steephead ravine forests of the Apalachicola River Bluffs in northern Florida is strongly influenced by position

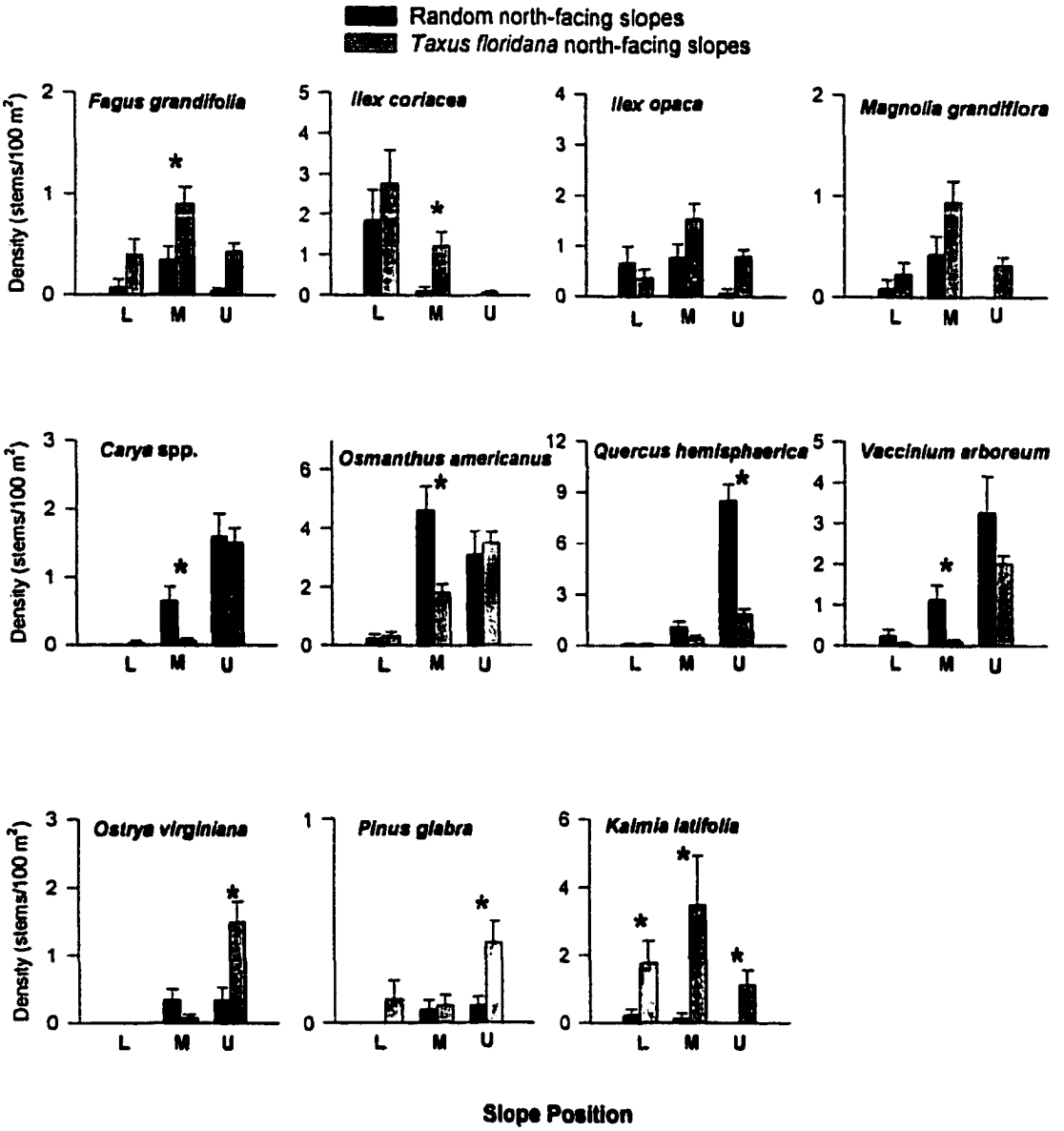

Figure 1.5. Densities (back-transformed ± Standard Error) of important woody species (stems ≥ 2 cm dbh) as a function of type of north-facing slope and slope position (L = Lower Slope, M = Midslope, U = Upper Slope). Asterisks denote significant differences at particular slope positions (Tukey-Kramer multiple comparisons of means, $P < 0.05$).

along ravine slopes. Although gradual changes do occur in abundances of tree species along steephead slopes, the lower slopes, midslopes, and upper slopes tend to be characterized by different species assemblages. Similar effects of slope position on forest community structure occur in steepheads of western Florida (Gibson 1992).

The relationship between tree species composition and slope position described in the current study, based on quantitative data, resembles distinctions made by previous qualitative studies; these identified lower slopes as dominated by hydric species, midslopes by mesic species, and upper slopes by xeric species (Clewell 1986, Wolfe et al. 1988, Platt and Schwartz 1990). Our results are inconsistent, however, with presettlement vegetation of the immediate area inferred from several other sources. Survey records from neither the Apalachicola River Bluffs region (Delcourt and Delcourt 1977) nor other areas in close proximity to the Apalachicola River Bluffs (Schwartz 1994) indicate an upslope oak-hickory zone. Likewise, descriptions of early naturalists do not indicate abundant oaks and hickories (e.g., Harper 1914). The dominance of oaks and hickories in a large upslope zone thus suggests a change in forest tree composition along ravine slopes within the past century (also see Clewell 1986).

Aspect had little effect on tree species densities in steephead ravine forests of the Apalachicola River Bluffs. In our study, the densities only of two typical upslope species, *Quercus hemisphaerica* and *Vaccinium arboreum*, were affected by aspect; more stems of these species occurred on random

north-facing slopes than random south-facing slopes. Differences in fire history along north- and south-facing slopes potentially could affect densities of these trees along the upper slopes. Possibly cooler, more mesic north-facing slopes are less susceptible to fire than drier south-facing slopes.

The presence of *Taxus floridana* on north-facing slopes was associated with increased densities of primarily evergreen species in the Apalachicola River Bluffs. *Ilex coriacea*, *I. opaca*, *Fagus grandifolia*, *Kalmia latifolia*, *Magnolia grandiflora*, and *Pinus glabra*, as well as the deciduous *F. grandifolia*, were more abundant along north-facing slopes containing *T. floridana*. This pattern was especially pronounced along midslopes. Thus, forests in midslope regions of north-facing steephead slopes that contain adult *T. floridana* more closely resembled the classical definition of the souther mixed species hardwood forest type (sensu Quarterman and Keever 1962) than forests at the same or different positions along other slopes in the Bluffs region. The basic physiognomy of this forest type, which involves a mixture of evergreen and deciduous species in the overstory and understory, is similar throughout the Southeastern Coastal Plain (see Marks and Harcombe 1975, 1981, Glitzenstein et al. 1986, Platt and Schwartz 1990, Quigley and Platt 1996; for review see Batista and Platt 1997).

We suggest two, nonmutually exclusive, explanations of the current patterns of the distribution of *T. floridana* and associated, mostly evergreen species, in the Apalachicola River Bluffs steepheads. The first hypothesis involves the existence of unique, naturally occurring, mesic microsites in

steephead ravines. North-facing slopes with adult *T. floridana* could represent a unique subset of north-facing slopes containing abundant evergreen understory species. Low soil nutrients and/or pH at local scales could in part be responsible, especially if also associated with wooded seeps (A. Clewell, personal communication). Such soil characteristics have been proposed to be associated with increased proportions of evergreen trees (Monk 1965, 1966). Although not directly analyzed, steep slope angles along north-facing midslopes with *T. floridana* also could be important in distinguishing these areas (see Gibson 1992). The patchy distribution of midslopes with conditions favorable for evergreen understory species throughout steepheads of the Apalachicola River Bluffs could result in naturally subdivided populations of *T. floridana* and associated species. Thus, the existence of *T. floridana* (and other evergreen species) on north-facing steephead midslopes of the Apalachicola River Bluffs might be a function of patchily distributed seepage or mesic conditions on steep slopes with particular soil conditions within raviens (as often suggested). Such a scenario, however, does not fully agree with historical data because the oak-hickory zone in nearby upper and midslope regions does not appear to have been present historically.

A second hypothesis involves effects of recent anthropogenic disturbances. Such disturbances might have affected midslopes of steephead ravines in ways that have restricted the distribution of *T. floridana* and other evergreen species. The pine savannas between ravine systems and along upper slopes (see Platt 1999) were logged in the early 1900's. Accelerated

erosion folowing clearcutting of *Pinus palustris* could have produced a disturbance regime along some upper slopes and adjacent midslopes that involved many more treefall gaps along steep, unstable slopes, and resulted in more xeric soil conditions. In addition, suppression of creeping hammock fires (Blaisdell et al. 1974), which would have most likely originated in adjacent upland pine savannas (see Platt et al. 1988, 1991), could have resulted in the release and expansion of oaks, hickories, and xeric understory shrubs (see Rebertus et al. 1993), especially along north-facing slopes. Thus, although *T. floridana* was not a very common species historically (Harper 1914), it may have once been more widely distributed along slopes along with other evergreen species. These species may now be more restricted as a result of human-induced changes in disturbance regimes. These same changes also could have produced the differences in forest tree composition along slopes that emerged from comparison of results of our study with studies based on land office survey records.

CHAPTER 2

DEMOGRAPHY OF *TAXUS FLORIDANA*, A RARE UNDERSTORY CONIFER

INTRODUCTION

Recruitment has served as a focal point for the conservation of rare plant species. Recruitment limitation, which characterizes all rare plants, can be responsible for small local population sizes or for confinement to particular habitats or geographic ranges (i.e., characteristics of species rarity sensu Rabinowitz 1980, Rabinowitz et al. 1986). In some instances, recruitment limitation has been postulated as the reason that a plant is rare, and possibly also in decline (Mehrhoff 1989, Aspinwall and Christian 1992). Thus, it may be important for a rare plant to experience even brief periods of high recruitment.

Predictions of long-term population growth rates are important for the conservation of rare plant species. Understanding how an endemic plant with local (i.e., within population or subpopulation) recruitment limitation may exhibit positive population growth within its small geographic range might facilitate development of conservation strategies, especially if populations throughout its range are in decline. Such plant species are often a primary focus of conservation efforts (e.g., Yates et al. 1996, Parsons and Zedler 1997, Tremblay et al. 1998, and many others). Multi-year demographic studies of endemic plants throughout their entire geographic range, however, have only rarely been undertaken for endemic herbs (Menges 1990, Oostermeijer et al. 1996, Allphin and Harper 1997, Kephart and Paladino 1997, Floyd and Ranker

1998, Quintana-Ascencio et al. 1998), and such studies for endemic woody plants are lacking.

In this study, we investigated the demography of *Taxus floridana* Nutt., a rare, slow-growing, long-lived coniferous understory shrub endemic to wooded ravine forests of the Apalachicola River Bluffs region of northern Florida, U.S.A. (Redmond 1984, Platt and Schwartz 1990, Kwit et al. 1998). During the previous decade, little seedling establishment has been observed in *T. floridana* populations (W. J. Platt, personal observation). Over a four year period, during which substantial seedling recruitment occurred only once, we gathered demographic information from three populations located in three separated ravines. Survival, growth, and recruitment were used to describe ravine- and size-related demographic trends. We tested explicitly whether certain demographic characteristics varied spatially and/or temporally throughout its range. We then utilized these demographic data to predict the future status of *T. floridana* using periodic matrix population models (Skellam 1966). Such a modeling approach allowed investigation of the effects of changes in frequencies and the magnitude of episodic, or re-occurring and high, recruitment on population growth rates. We also hypothesized how certain types of rare plant species might persist regardless of predicted population growth rates. Such advances are crucial to the continued study of rare species biology (see Schemske et al. 1995).

METHODS

Study Area

Hardwood ravine forests of the Apalachicola River bluffs region of northern Florida occur along creek drainages on the east side of the Apalachicola River in Liberty and Gadsden Counties. These forests are typically situated between and dissected by upland sandy clayhills and sandhills that were historically occupied by longleaf pine (*Pinus palustris*) savannas. From north to south, soils of these hardwood ravine forests progress from Miocene sandy clays in gully-eroded ravines to Pleistocene sands in steepheads (Means 1975, Platt and Schwartz 1990). Mean monthly temperatures range from a maximum of 27°C in July to a minimum of 11°C in January; mean annual rainfall is 1420 mm, with October and November typically being the driest months (NOAA 1982).

Vegetation of hardwood ravine forests of the Apalachicola River bluffs closely resembles that found in other hardwood forests throughout the Southeastern Coastal Plain (see Marks and Harcombe 1981, Platt and Hermann 1986, White 1987, Batista and Platt 1997). A high diversity of deciduous and evergreen species comprises both the overstory and understory (Platt and Schwartz 1990). The overstory of upper slopes is dominated by oaks *Quercus* sp. (oaks) and *Carya* sp. (hickories); the midslopes by *Fagus grandifolia* (American beech) and *Magnolia grandiflora* (southern magnolia); and lower slopes by *Magnolia virginiana*, *Nyssa biflora*, and others (Clewell 1986, Kwit et al. 1998). The understory is comprised of variety of understory

trees and shrubs, including two endemic species of the family Taxaceae, *Torreya taxifolia* (see Schwartz and Hermann 1993, 1999, Schwartz et al. 1995) and *Taxus floridana*.

Taxus floridana is a dioecious, evergreen, understory conifer that is primarily located along lower- and midslopes of hardwood ravine forests of the Apalachicola River bluffs. Populations are scattered and subdivided, and occasionally are characterized by stem counts in excess of 1000 per hectare. *Taxus floridana* is commonly found growing alongside high densities of other evergreen understory species, such as *Ilex coriacea*, *Ilex opaca*, and *Kalmia latifolia*; this pattern is especially pronounced in steepheads (Kwit et al. 1998). Despite the ability to reproduce asexually via branch layering (see Redmond 1984) and to produce seeds, little recruitment of small stems had occurred during the decade prior to our study (C. Kwit and W. J. Platt, personal observation).

Data Collection

A total of six study plots (each approximately 0.25 ha) were established in June 1995 to measure demographic parameters of *T. floridana*. From north to south, two plots each were located along a tributary of Rock Creek in Torreya State Park (hereafter referred to as Rock Creek), along Long Branch, and along tributaries of Beaverdam Creek in The Nature Conservancy's Apalachicola Bluffs and Ravines Preserve (hereafter referred to as Beaverdam Creek). All *T. floridana* stems were tagged and measured for basal diameter and height. At the onset, approximately 2300 stems were tagged (see Fig. 2.1). Annual

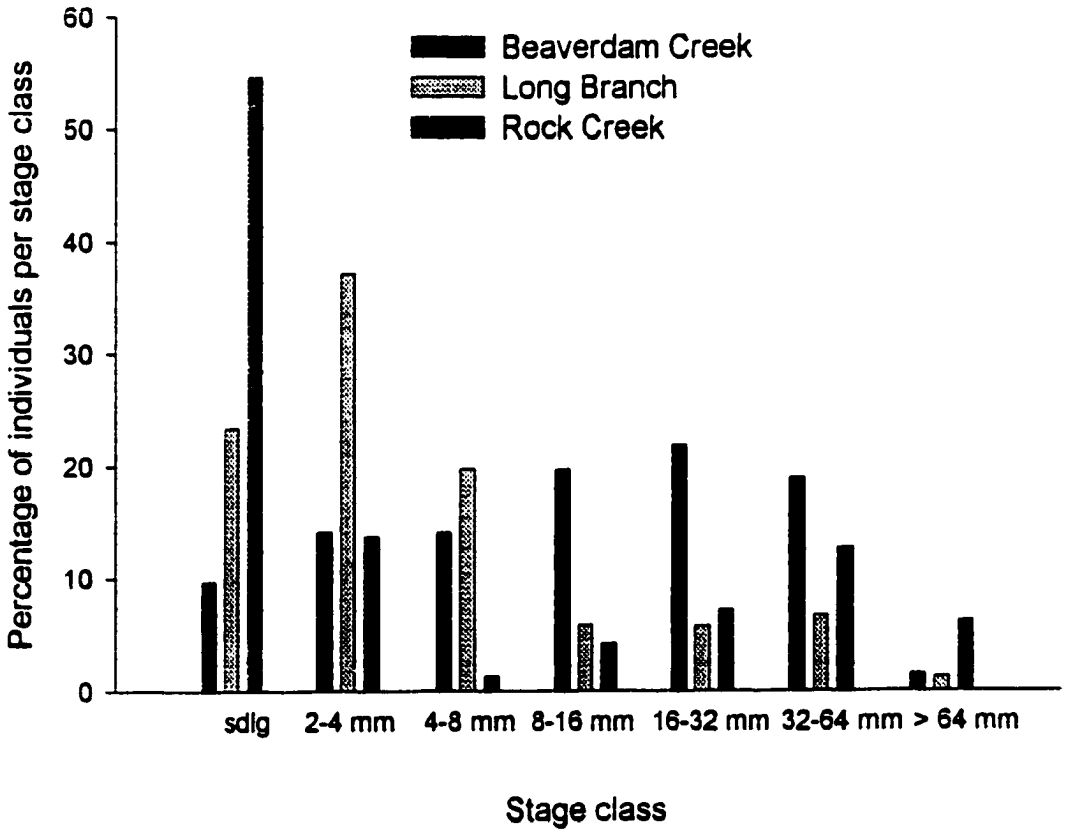

Figure 2.1. Stage class distributions of *Taxus floridana* stems tagged at the onset of the study in 1995. Data from plots within each ravine were pooled.

censuses of plots in 1996 through 1999 during late May/early June, the period coinciding with completion of seed germination, were used to record the survival of seedlings and the appearance of additional seedling recruitment. Survival of all other stems was documented in five of the six study plots during the same annual censuses due to excess erosion in one of the Long Branch plots.

Growth rates of *T. floridana* stems were estimated from cross sections of dead stems taken from each of the three ravines. A total of 30 cross sections, 10 from each ravine, of various sizes were cut at the base of each dead stem. Cross sections were sanded, and widths of annual rings were measured using a Henson tree ring analyzer (0.01 mm resolution) at the USGS National Wetland Center in Lafayette, Louisiana, USA.

Demographic Patterns and Analyses

Stage classification.—We chose to classify stem data by stage classes that reflected a combination of life history stages and stages based on stem size (see Fig. 2.2). The seedling stage was represented by non-woody green stems which took three years following seed germination to attain enough woody tissue to reach 2 mm diameter (C. Kwit, personal observation). All other stages were represented by exponentially increasing size classes, inclusive of the value on the left hand side (e.g., for the 2-4 mm stage class, 2 mm $\leq$ stem size $<$ 4 mm); this was done to increase sample sizes for more reliable survival probability estimates. Such a classification scheme is amenable to matrix population analyses.

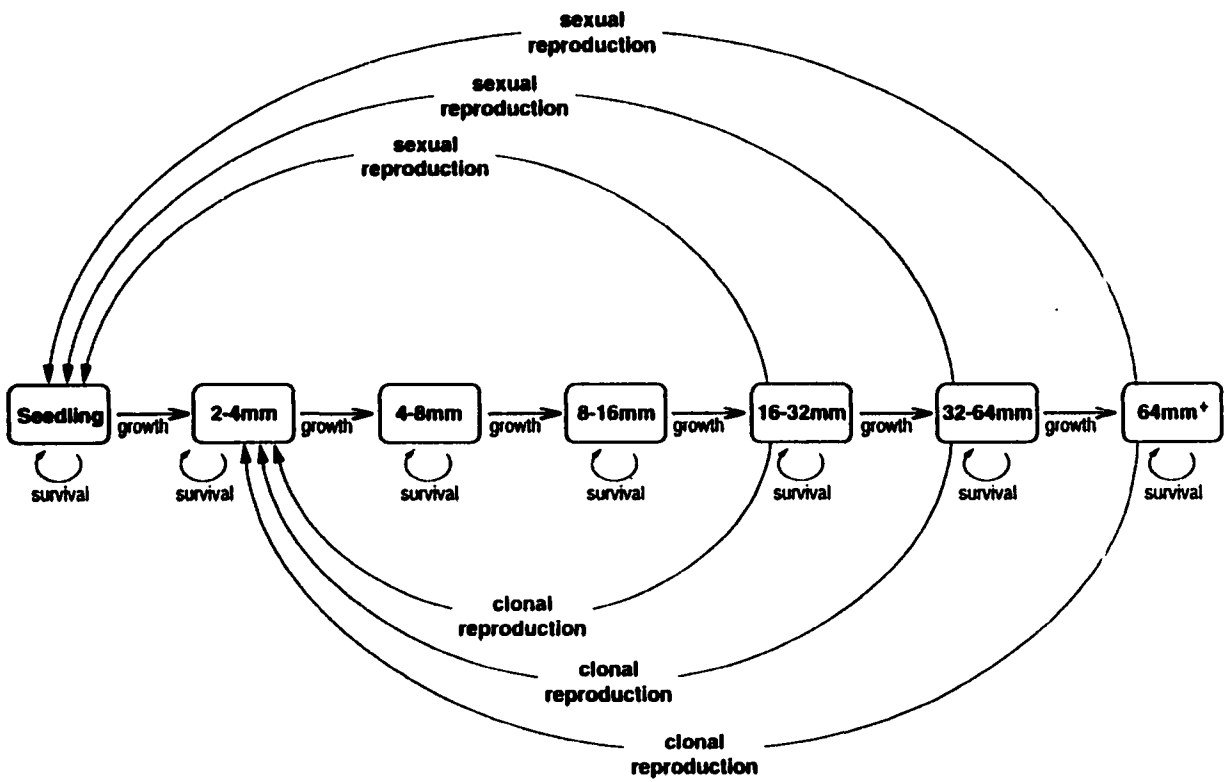

Figure 2.2. Life cycle graph of *Taxus floridana* stem demography. The nodes represent stages, and the arrows represent transitions between stages. Clonal reproduction via layering of stems and subsequent adventitious rooting was not observed during the course of our study.

Recruitment.—We tested for spatial (i.e., ravine), temporal (i.e., year), and interaction effects on the numbers (natural log transformed) of new seedlings found in all six study plots during the 1996-1999 annual censuses. Repeated measures analysis of variance of the general form $y_{ijk} = \mu + \alpha_i + d_{ij} + \tau_k + (\alpha\tau)_{ik} + e_{ijk}$ (Littell et al. 1996) where α_i refers to ravine, τ_k refers to time, d_{ij} is the random effect associated with the j^{th} plot in the i^{th} ravine, and e_{ijk} is the random error associated with the j^{th} plot in the i^{th} ravine, was used for this part of the investigation. To standardize plots, the sums of the 1995 log-transformed basal areas (mm^2) of reproductive *T. floridana* stems in each plot were used as covariates. We assumed a compound symmetry covariance structure, which entails homogeneous variance and a constant temporal correlation, two common features of a typical split-plot design. *A posteriori* comparisons were accomplished with appropriate contrasts and Tukey-Kramer pair-wise comparisons.

Fates of stems.—The fates of stems were determined at each census. At any particular census, seedlings from the prior census could experience one of three possible fates: growth into the 2-4 mm stage class, stasis within the seedling stage class, or death. For non-seedling stems in each non-seedling stage class, possible fates included solely survival and mortality;

To determine if fates of stems in each stage class were affected by ravine and year, we used loglinear analyses. Loglinear models are used to predict counts within contingency tables (see Agresti 1990, 1996). For each stage separately, we first fit a null model predicting that the fate, *F*, of individual

stems was independent of ravine, *R*, and year, *Y*, given the preset ravine x year interaction. The equation of this model is: $\log m_{ijk} = u + u_{R(i)} + u_{Y(j)} + u_{F(k)} + u_{RY(ij)}$, which can also be noted as (*RY*, *F*). To test for the effect of ravine on fate, we fit the model (*RY*, *RF*), which includes the term $u_{RF(ik)}$ added to the previous model. Differences in deviances of models from a fully saturated model (*RYF*) were used to obtain a G^2 statistic, which is χ^2 distributed, and this G^2 statistic was used to test for the effect of ravine. A similar approach was used to test for the effect of year on fate; differences in the deviances of the null (*RY*, *F*) and the model incorporating the effect of year (*RY*, *YF*) were used to test the effect of year.

Stem growth.—We tested the effect of ravine on the growth of individual dead stems through time. We modeled the diameters of individual stems as a linear function of age through the first 60 years of stem existence (when applicable) using random coefficient regression (Littell et al. 1996). The general form of the model is: $y_{ij} = a_i + x_{ij}b_i + e_{ij}$, where y_{ij} is the diameter at the j^{th} age of the i^{th} stem, *a* is analogous to an intercept coefficient, *b* is analogous to a slope coefficient, *x* refers to age, and e_{ij} is a normally distributed error term with mean 0 and an estimated variance. To test if growth rates were affected by ravine, an interaction term $x_{ij}R_kc_{ik}$, analogous to a slope adjustment, was added to the model, and a Type I *F* test was used to test its significance. Such a modeling approach can be used to estimate the growth rate (mm/year; i.e., a slope coefficient) of separate or effectively one population, depending on which model best fits the data.

Periodic Matrix Models

Construction of annual population matrices.—A total of twelve unique annual matrices (4 transition years and 3 ravines) were possible to describe the dynamics of the 7 stage classes (see Fig. 2.2) of *T. floridana* in our study. The matrix elements a_{ij} describe the transition rates of individuals from stage j at time t to any stage i at time $t + 1$. Entries of vital demographic rates of fertility (F), stasis (S), and growth (G) were considered unique when effects of ravine and/or time were significant in the preceding analyses. If ravine and/or time did not affect seedling recruitment or fates of stems, empirical data was pooled across the non-significant term(s). Specific details concerning the determination of specific matrix entries are outlined below.

Measures of fertility, or the reproductive output (seedlings/individual) of each sexually reproductive stage class, were assumed to be proportional to the diameter of adult plants since larger stems are capable of producing more seeds (C. Kwit, personal observation). Thus, if ravine and time were significant effects, the total number of new seedlings found at each annual census in each ravine would be divided by the sum of the diameters of reproductive stems in each ravine observed in 1995 to give an estimate of the annual "per-diameter" contribution to reproduction. This was then multiplied by the mean diameter of each reproductive stage class to provide an annual estimate F for each reproductive stage class in each ravine (see Huenneke and Marks 1987, Caswell 1989).

Stasis and growth entries for stems were determined, in part, by empirical data on the fates of stems. To determine the stasis and growth entries associated with seedlings, we used maximum likelihood estimates of empirical data on seedling fates. No direct data was obtained on the growth of individual non-seedling stems from one stage class to the next. Thus, maximum likelihood estimates of the fates of stems of non-seedling stage classes were analogous to annual probabilities of survival, or σ_i. Obtaining estimates of stasis and growth for non-seedling stage classes required such estimates, along with estimates of probabilities of growth for surviving individuals, γ. Estimates for γ involved estimates of the time (in years) spent in each stage class, T_i, which were obtained using inverse prediction (Neter et al. 1990) from the analysis of diameters of individual stems as a function of age, such that

$$\gamma_i = \frac{(\sigma_i / \lambda)^{T_i} - (\sigma_i / \lambda)^{T_i - 1}}{(\sigma_i / \lambda)^{T_i} - 1}$$

(see Caswell 1989, pp. 83-85). In the above equation we assumed λ, or population growth rate, to be equal to one (as Crouse et al. 1987), and then calculated growth and stasis entries as $G = \sigma\gamma$ and $P = \sigma(1 - \gamma)$.

The periodic matrix model.—The dynamics of each *T. floridana* population over the four year period can be described by the periodic matrix product of sequential population projection matrices:

$$\mathbf{n}(t + 4) = [\mathbf{B}^{(4)}\mathbf{B}^{(3)}\mathbf{B}^{(2)}\mathbf{B}^{(1)}]\mathbf{n}(t) = \mathbf{A}^{(1)}\mathbf{n}(t)$$

where the superscripts on the **B** matrices refer to individual years, and the superscript on the **A** matrix refers to the phase at which the projection starts. The product matrix $\mathbf{A}^{(1)}$ projects the population through the four year cycle, and the long-term population growth rate over the period of the cycle is given by the dominant eigenvalue of $\mathbf{A}^{(1)}$. The mean annual growth rate, λ, is simply the t^{th}, or 4^{th} root of the dominant eigenvalue of $\mathbf{A}^{(1)}$.

Within this framework, we examined first whether the demography of *T. floridana* populations would be predicted to exhibit positive long-term growth rates ($\lambda > 1$) assuming that such a four year cycle would continue to occur in the future. If this was not predicted, we intended to examine the magnitude of episodic seedling recruitment occurring once every four years (as observed in year one of our study) necessary in each population such that $\lambda \approx 1$. Finally, we investigated the effect of increasing the period between successive episodic recruitment years on λ. To accomplish this, we assumed that matrices following the fourth year ($\mathbf{B}^{(4)}$) describing the demography of *T. floridana* populations would always be represented by year 3 ($\mathbf{B}^{(3)}$). Thus, for example, the dynamics of each *T. floridana* population over a cycle with five years between episodic recruitment events would be described by

$$\mathbf{n}(t+5) = [\mathbf{B}^{(3)}\mathbf{B}^{(4)}\mathbf{B}^{(3)}\mathbf{B}^{(2)}\mathbf{B}^{(1)}]\mathbf{n}(t) = \mathbf{A}^{(1)}\mathbf{n}(t).$$

Eigenvalues of periodic matrix products were computed using the program MATLAB.

RESULTS

Demographic Patterns

Recruitment.—The number of new *Taxus floridana* seedlings was influenced primarily by year (Table 2.1). The effect of year was highly significant ($P < 0.0001$), while ravine and interactive effects were non-signficant. Based on adjusted Tukey-Kramer pairwise comparisons, numbers of new seedlings were highest in 1996, lower in 1997 and 1998 ($P = 0.5298$), and lowest in 1999 (Fig. 2.3). Seedling numbers from 1996 were significantly higher than all other years (*a posteriori* contrast, $F = 270.50$, $P < 0.0001$), and approximately one order of magnitude greater than the average of the proceeding three years.

Fates of stems.—The fates of stages of *T. floridana* were affected by ravine and time in different manners. Fates of seedlings were significantly affected by both ravine and time, while fates of small sized stems (2-4 mm and 4-8 mm) were significantly affected by ravine (Table 2.2).

Stem growth.—Predicted diameters of individual *T. floridana* stems through time, as measured from cross-sections, were well described by a linear model (Fig. 2.4). Stem diameter growth was estimated at 0.8117 mm/year based on the overall slope coefficient. Stem diameter growth did not differ among ravines ($F_{2,27} = 1.07$, $P = 0.3581$).

Matrix Model of Population Growth

Construction of annual population matrices.—Annual transition matrices for each population of *T. floridana* were constructed based on the significance

Table 2.1. Repeated measures analysis of variance tests for effects of ravine, year, and ravine x year interaction on the number of seedlings (natural log transformed) of *Taxus floridana* per plot (≈ 0.25 ha). The covariate in the model was the per-plot sum of natural log transformed basal areas (mm^2) of reproductive stems (stems ≥ 16 mm diameter).

Source	$DF_{numerator}$	$DF_{denominator}$	Type III F	Prob > F
Covariate	1	2	0.56	0.5317
Ravine	2	2	4.65	0.1770
Year	3	9	100.94	0.0001
Ravine x Year	6	9	1.8	0.2057

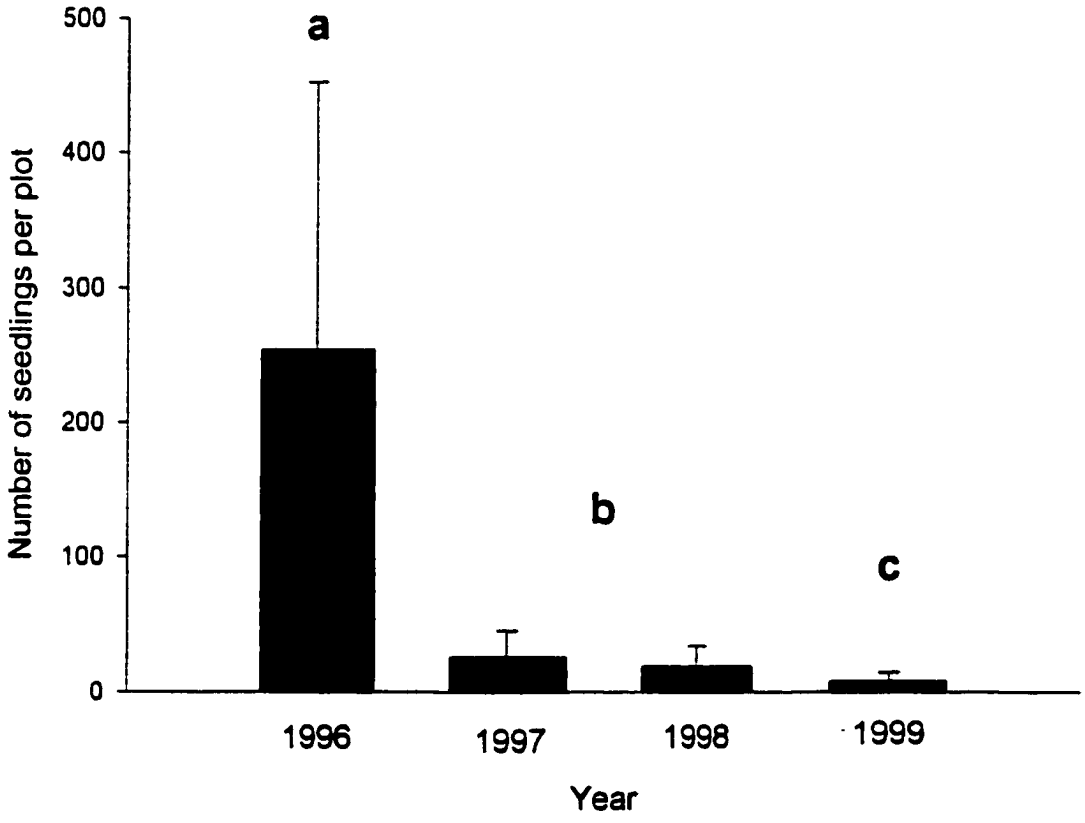

Figure 2.3. Number (back-transformed) of *Taxus floridana* seedlings per plot (each ≈ 0.25 ha) in each of the four censuses. Data is displayed as least squares means ± standard error (back-transformed), which takes the covariate (sum of natural log-transformed basal areas [mm^2] of reproductive stems) into account. Letters represent significant ($P < 0.05$) yearly differences based on adjusted Tukey-Kramer pairwise comparisons.

Table 2.2. Transition matrices (**B**) for sampled populations of *Taxus floridana*. Stages (except for sdlg) are in mm.

Stage at time *t*+1	Stage at time *t*						
	sdlg	2-4	4-8	8-16	16-32	32-64	64+
a. Rock Creek							
			1995-1996				
sdlg	0.2367	0	0	0	4.287	8.574	17.148
2-4	0	0.493	0	0	0	0	0
4-8	0	0.2213	0.764	0	0	0	0
8-16	0	0	0.1591	0.8229	0	0	0
16-32	0	0	0	0.0428	0.9189	0	0
32-64	0	0	0	0	0.0272	0.9625	0
64+	0	0	0	0	0	0.0157	0.9565
			1996-1997				
sdlg	0.2377	0	0	0	0.552	1.103	2.207
2-4	0	0.493	0	0	0	0	0
4-8	0	0.2213	0.764	0	0	0	0
8-16	0	0	0.1591	0.8229	0	0	0
16-32	0	0	0	0.0428	0.9189	0	0
32-64	0	0	0	0	0.0272	0.9625	0
64+	0	0	0	0	0	0.0157	0.9565
			1997-1998				
sdlg	0.1645	0	0	0	0.354	0.708	1.416
2-4	0.026	0.493	0	0	0	0	0
4-8	0	0.2213	0.764	0	0	0	0
8-16	0	0	0.1591	0.8229	0	0	0
16-32	0	0	0	0.0428	0.9189	0	0
32-64	0	0	0	0	0.0272	0.9625	0
64+	0	0	0	0	0	0.0157	0.9565
			1998-1999				
sdlg	0.0294	0	0	0	0.152	0.304	0.609
2-4	0.2941	0.493	0	0	0	0	0
4-8	0	0.2213	0.764	0	0	0	0
8-16	0	0	0.1591	0.8229	0	0	0
16-32	0	0	0	0.0428	0.9189	0	0
32-64	0	0	0	0	0.0272	0.9625	0
64+	0	0	0	0	0	0.0157	0.9565

Table 2.2. Continued.

Stage at time *t*+1	Stage at time *t*						
	sdlg	2-4	4-8	8-16	16-32	32-64	64+
b. Long Branch							
			1995-1996				
sdlg	0.1979	0	0	0	4.287	8.574	17.148
2-4	0	0.5674	0	0	0	0	0
4-8	0	0.3469	0.7683	0	0	0	0
8-16	0	0	0.1642	0.8229	0	0	0
16-32	0	0	0	0.0428	0.9189	0	0
32-64	0	0	0	0	0.0272	0.9625	0
64+	0	0	0	0	0	0.0157	0.9565
			1996-1997				
sdlg	0.2144	0	0	0	0.552	1.103	2.207
2-4	0	0.5674	0	0	0	0	0
4-8	0	0.3469	0.7683	0	0	0	0
8-16	0	0	0.1642	0.8229	0	0	0
16-32	0	0	0	0.0428	0.9189	0	0
32-64	0	0	0	0	0.0272	0.9625	0
64+	0	0	0	0	0	0.0157	0.9565
			1997-1998				
sdlg	0.1594	0	0	0	0.354	0.708	1.416
2-4	0.0249	0.5674	0	0	0	0	0
4-8	0	0.3469	0.7683	0	0	0	0
8-16	0	0	0.1642	0.8229	0	0	0
16-32	0	0	0	0.0428	0.9189	0	0
32-64	0	0	0	0	0.0272	0.9625	0
64+	0	0	0	0	0	0.0157	0.9565
			1998-1999				
sdlg	0.0653	0	0	0	0.152	0.304	0.609
2-4	0.1187	0.5674	0	0	0	0	0
4-8	0	0.3469	0.7683	0	0	0	0
8-16	0	0	0.1642	0.8229	0	0	0
16-32	0	0	0	0.0428	0.9189	0	0
32-64	0	0	0	0	0.0272	0.9625	0
64+	0	0	0	0	0	0.0157	0.9565

Table 2.2. Continued.

Stage at time t+1	Stage at time t						
	sdlg	2-4	4-8	8-16	16-32	32-64	64+
c. Beaverdam Creek							
			1995-1996				
sdlg	0.1154	0	0	0	4.287	8.574	17.148
2-4	0	0.5532	0	0	0	0	0
4-8	0	0.3189	0.7044	0	0	0	0
8-16	0	0	0.1029	0.8229	0	0	0
16-32	0	0	0	0.0428	0.9189	0	0
32-64	0	0	0	0	0.0272	0.9625	0
64+	0	0	0	0	0	0.0157	0.9565
			1996-1997				
sdlg	0.082	0	0	0	0.552	1.103	2.207
2-4	0	0.5532	0	0	0	0	0
4-8	0	0.3189	0.7044	0	0	0	0
8-16	0	0	0.1029	0.8229	0	0	0
16-32	0	0	0	0.0428	0.9189	0	0
32-64	0	0	0	0	0.0272	0.9625	0
64+	0	0	0	0	0	0.0157	0.9565
			1997-1998				
sdlg	0.1071	0	0	0	0.354	0.708	1.416
2-4	0	0.5532	0	0	0	0	0
4-8	0	0.3189	0.7044	0	0	0	0
8-16	0	0	0.1029	0.8229	0	0	0
16-32	0	0	0	0.0428	0.9189	0	0
32-64	0	0	0	0	0.0272	0.9625	0
64+	0	0	0	0	0	0.0157	0.9565
			1998-1999				
sdlg	0.0767	0	0	0	0.152	0.304	0.609
2-4	0.0767	0.5532	0	0	0	0	0
4-8	0	0.3189	0.7044	0	0	0	0
8-16	0	0	0.1029	0.8229	0	0	0
16-32	0	0	0	0.0428	0.9189	0	0
32-64	0	0	0	0	0.0272	0.9625	0
64+	0	0	0	0	0	0.0157	0.9565

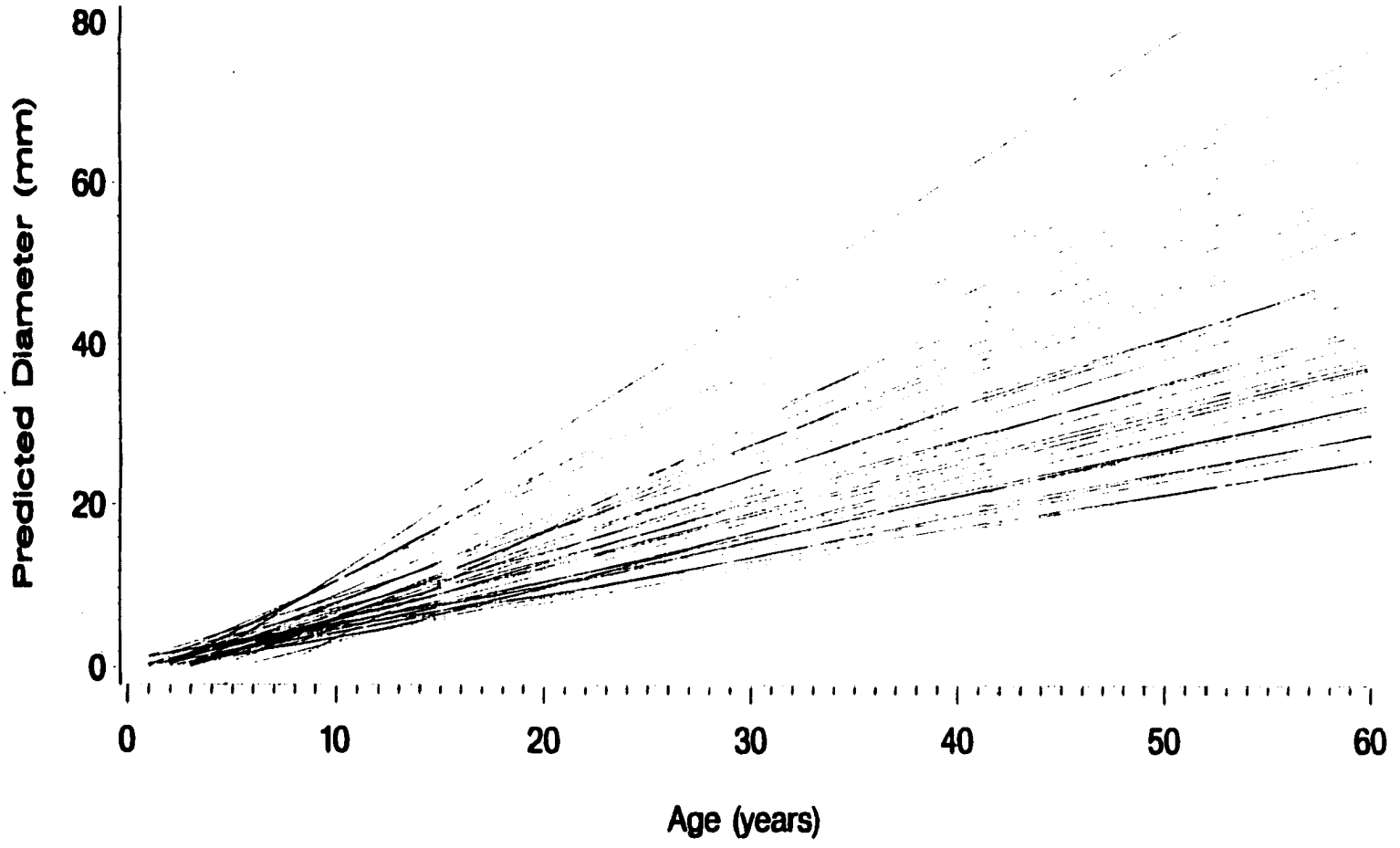

Figure 2.4. Predicted individual *Taxus floridana* stem diameters as a function of stem age. Predictions are from a random coefficient linear regression model. Data is based on aged and measured cross sections of dead stems from each sampled ravine.

(or lack thereof) of year and ravine on seedling recruitment and fates of stems, and on the significance of ravine on stem growth. Since seedling recruitment was only significantly affected by year, all populations of *T. floridana* were characterized by the same set of unique yearly fertility rates. Since both year and ravine significantly affected the fates of seedlings, rates of seedling stasis and growth were estimated via maximum likelihood estimation of empirical data for each ravine and year combination. Estimates of annual probabilities of survival (σ) in each individual ravine were estimated via maximum likelihood estimation of empirical data in the 2-4 and 4-8 mm stage classes due to the significant effect of ravine. All other estimates of σ for non-seedling stages were determined via maximum likelihood of empirical data pooled over ravines and years. As the growth rates of stems did not significantly differ among ravines, annual growth probabilities (γ) for individual non-seedling stages were considered to be the same in each year and ravine. Thus, rates of stasis and growth for individual non-seedling stages only differed by ravine for the 2-4 and 4-8 mm stage classes, and were the same across all years in the remaining non-seedling stage classes.

Entries within annual transition matrices reflected the significant differences in ravines and years (Table 2.3). Fertilities for the 1996 (year 1) matrix reflected the observed "boom" in recruitment, and ranged from 4.287 seedlings per 16-32 mm individual to 17.148 seedlings per individual $\geq$ 64 mm. Fertilities for the other three years were lower, with the lowest values in the 1999 (year 4) matrix, where values ranged from 0.152 seedlings per 16-32 mm

Table 2.3. G^2 values from loglinear analyses of effects of ravine and year on fates of *Taxus floridana* stems. Tests were performed on each stage class separately. Tests for effects of ravine were based on χ^2 distribution with 14 d.f., and tests for effects of year were based on a χ^2 distribution with 21 d.f.

Stage	Ravine	Year
sdlg	53.9721*	352.6135*
2-4	64.1882*	18.4213
4-8	56.8992*	11.6079
8-16	22.6919	3.9174
16-32	18.5700	2.1020
32-64	2.0669	2.1823
64+	10.1053	1.9802

* $P < 0.05$

individual to 0.609 seedlings per individual ≥ 64 mm. Overall seedling survival rates (stasis + growth rate entries) were consistently lower in the Beaverdam population (≈ 10%) than in Long Branch and Rock Creek (≈ 20%). Seedling growth rates were highest in the fourth year for each population, reflecting the higher survival of seedlings from the 1996 cohort which eventually grew into the 2-4 mm stage class. For the 2-4 and 4-8 mm stage classes, overall survival rates were highest in Long Branch; overall survival rates for the 2-4 mm stage class were lowest in the Rock Creek population, while those for the 4-8 mm stage class were lowest in the Beaverdam Creek population.

Periodic matrix models.—The projected annual rate of increase, or λ, for all three populations of *T. floridana* based on their demography over the four year period was < 1. Values of λ were slightly < 1 and ranged from 0.9664 in Beaverdam Creek, to 0.9764 in Long Branch, to 0.9769 in Rock Creek. Thus, if all three populations of *T. floridana* were to exhibit growth, survival, and fertility rates as those hypothesized to characterize its recent demography, populations would decline in the long term.

Exceptional increases in fertility rates during years of episodic recruitment (i.e., in Year 1 of the annual population matrices) were necessary to result in increasing population growth. In our study, the year of high recruitment was higher than other years by approximately one order of magnitude. Years of high recruitment occurring once every four years would need to be characterized by fertility rates of an over two orders of magnitude increase in

Long Branch and Rock Creek, and by an over three orders of magnitude increase in Beaverdam Creek for net positive population growth rates.

Increasing the period of time between high fertility years did not dramatically affect *T. floridana* population growth rates (Fig. 2.5). The largest changes in λ as the time between high fertility years increased occurred in the Rock Creek population. However, the predicted value of λ in Rock Creek when the period between high recruitment was 10 years was higher than that predicted in Beaverdam Creek when the period between observed high recruitment was four years.

Discussion

The demography of *Taxus floridana* populations throughout its range over the four years of study was not sufficient for future long-term population growth. Present day populations may therefore be simply experiencing slow long-term population declines, despite annually variable and sometimes episodically high recruitment. It is also possible, though, that populations of *T. floridana* exhibit a 'remnant' (sensu Eriksson 1996) population structure throughout its range; our study may have captured demographic information resulting from low quality habitats at the current time. This would imply that net-positive long-term population growth might result if high quality periods are experienced. This could be a function of long-term, or perhaps even short-term, changes in vital demographic rates that were not observed within the time frame of our study.

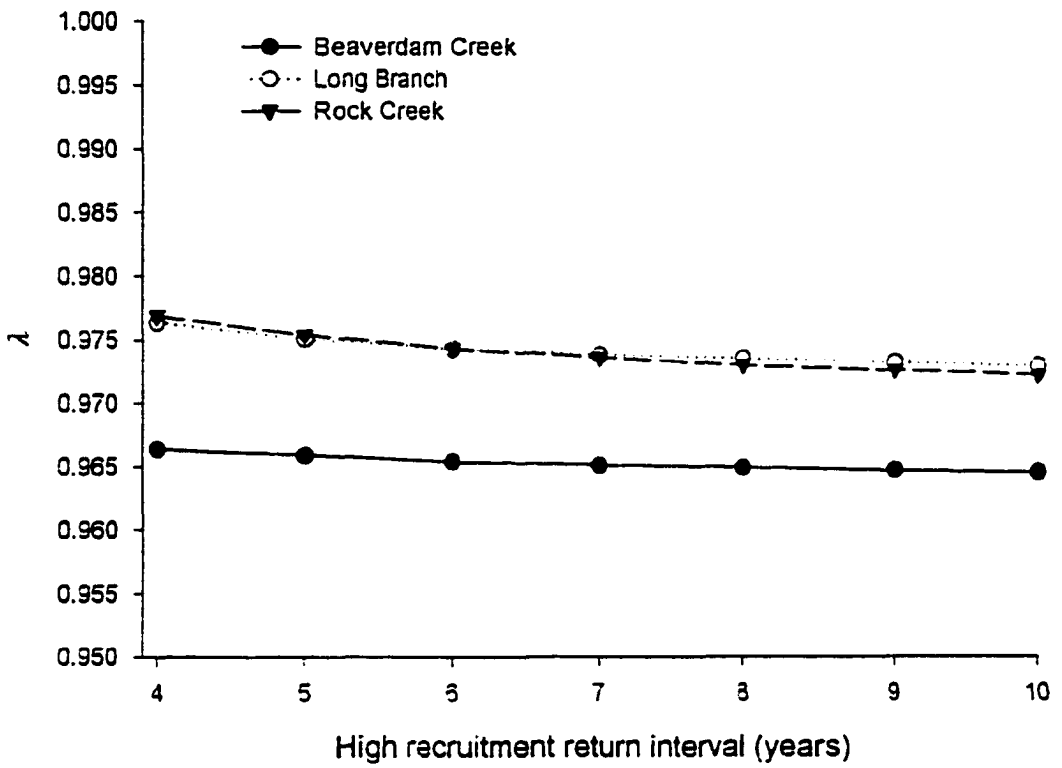

Figure 2.5. Relationship between annual population growth rates (λ) for *Taxus floridana* and time between successive high recruitment years. Estimates of population growth rates are based on eigenanalysis of periodic matrix products.

Projected long-term population declines based on our field study of *T. floridana* demography may also be due to recent anthropogenic changes within its habitat. In steephead ravines in the southern portion of its range, *T. floridana* is found with high densities of *Fagus grandifolia* and *Magnolia grandiflora* (Kwit et al. 1998), two overstory trees typifying southern mesic hardwood forests (Platt and Schwartz 1990) thought once to be more widespread in the Apalachicola River Bluffs. The present day existence of oak-hickory forests not evident in original public land office surveys (Delcourt and Delcourt 1977), especially along upper and midslopes of ravines, could be the result of a combination of events, including fire suppression and clearcutting of upland longleaf pine (*Pinus palustris*) sand/clayhills and increased slumping of ravines (Platt and Schwartz 1990). This in turn may have resulted in changed site conditions and less suitable habitat available within ravines for *T. floridana* (Kwit et al. 1998). Localized, less rapidly declining subpopulations within ravines may be all that remains of *T. floridana* populations that may have been more widespread several centuries ago.

Regardless of the reason that populations of *T. floridana* are predicted to decline, estimates of λ were only slightly less than one. High survival of adult stems, which characterizes a number of other woody understory species in tropical (Lieberman and Lieberman 1987, Condit et al. 1995) and temperate regions (Cipollini et al. 1994, Abe et al. 1998), including other species of *Taxus* (e.g., *Taxus brevifolia*; see Busing and Spies 1995), would likely result in slow population declines. *Taxus floridana* may therefore be an excellent example of

a species that can persist for long periods of time during its population decline (see Mangel and Tier 1994).

The potential for net-positive population growth for *T. floridana* does not appear to be limited solely by seedling recruitment. Despite the potential for *T. floridana* to persist for long periods of time, periodic annual increases in seedling recruitment alone are not predicted to result in net-positive population growth. Even if high seedling recruitment and overall seedling survival such as that observed in Year 1 of our study were to occur consistently every year, *T. floridana* would still be predicted to experience long-term population declines (results not shown). Conservation efforts based on aiding *T. floridana* seedling recruitment and establishment alone are likely not to be very useful. This finding is somewhat surprising considering that recruitment limitation has been a focal point of study for other species of *Taxus* (Hulme 1996, Minore et al. 1996). However, other options, such as increasing adult survivorship, may also not be a viable conservation strategy. Survival of these individuals is high to begin with, especially in reproductively mature adults, and preventing potentially random mortality of adult stems may be an unattainable goal (see Silvertown et al. 1996). Conservation efforts for *T. floridana* and other long-lived, slow-growing species hypothesized to be slowly declining are more likely to benefit from increased overall survival and growth of juvenile individuals. Thus, juvenile stems may be appropriate targets for future study (e.g., prevention from overgrazing by deer, study of effects of light gaps on growth and survival).

Long-term net-positive growth of *T. floridana* populations may still result from episodic establishment. Episodic clonal recruitment, which was not observed within the course of our study, could result in persistence via bypassing the seedling population bottleneck. Layering of branches by periodic disturbances such as frequent hurricanes (Batista and Platt 1997) and slope slumping is known to occur in *T. floridana* (Redmond 1984, Platt and Schwartz 1990), and has been documented in other understory species (Greig 1993, O'Dea et al. 1995). It is therefore possible that long-term net-positive growth of *T. floridana* populations would be facilitated by such disturbances.

Periods of high seedling recruitment are still potentially important for the persistence of *T. floridana*. The only seedlings exhibiting notable growth into the 2-4 mm stage class were represented by the high seedling recruitment cohort. High seedling survival following years of high recruitment has been noted a long-lived understory herb (Horvitz and Schemske 1995), and is often an assumed outcome of masting in woody plants (Kelly 1994, and references therein). Therefore, annual periods of high recruitment may delay local population extinction. The existence of *T. floridana* throughout the landscape is also possible if propagules during high recruitment years are more likely to be dispersed to demographically more favorable areas within ravines. Such a metapopulation model differs from the population model we investigated, in which we did not incorporate spatial and/or temporal demographic variation within ravines. The dynamic disturbance regime within ravine forests of the Apalachicola River Bluffs (see Platt and Schwartz 1990) provides some

justification for this suggestion. Slow-growing, long-lived plants, however, tend not to be characterized by metapopulation structure.

The apparent lack of consistent recruitment and seedling establishment in certain rare plants may not necessarily lead to long-term population decline. As long as a species is not concurrently confined to a restricted habitat in a small geographic range and represented by very few individuals, the inability to produce new stems may not be detrimental. For potentially long-lived plants endemic to small geographic areas, episodic recruitment may postpone local population extinction. However, from a conservation perspective, net-positive population growth is more likely to depend upon changes in survival and growth of juvenile stems.

CHAPTER 3

EFFECTS OF GAPS AND GAP HISTORY ON UNDERSTORY TREES IN A HURRICANE DISTURBED MIXED-SPECIES HARDWOOD FOREST

INTRODUCTION

Treefall gaps in closed canopy forests are important for persistence of many woody understory species that never reach canopy height (hereafter, understory species). For such understory species, treefall gaps can promote higher seed germination and seedling growth rates (Cipollini et al. 1994). In addition, gaps also provide spatial locales where growth rates (Denslow et al. 1990, Pascarella and Horvitz 1998, Abe et al. 1998) and fruit and seed production (Levey 1990, Pascarella and Horvitz 1998, Abe et al. 1998) are greater than in nearby areas under closed canopy. Thus, treefall gaps may influence persistence of woody understory species in forests that form closed canopies in a number of different ways.

The demographic response of understory species to disturbances may also depend on the different histories experienced by individual stems in localized areas. Thus, although advance recruits of understory species likely require treefall gaps to progress out of the seedling bank, it is also possible that the response to a disturbance in any particular area may be a function of previous disturbance history, such as time since previous gap formation. For example, following gap formation, sufficient time may need to elapse before the seedling bank can build to high levels. Few long-term or chronosequential studies have addressed these potential effects of prior gap history (but see Marks and Gardescu 1998).

Hurricanes are prominent disturbances that create treefall gaps and increase light levels in temperate and subtropical hardwood forests throughout the world. Following hurricanes, increased light directly reaches the understory stratum below areas of canopy removal, and diffuse light may also reach adjacent and nearby areas (see Poulson and Platt 1990) which may be under closed canopy or in pre-existing gaps at various stages of closure. Thus, large portions of forests have the potential to be affected by hurricanes. This is likely to occur in mixed species hardwood forests of the Southeastern Coastal Plain of the United States where hurricanes frequently impact forests (on average once every 20 years; Batista and Platt 1997) that exhibit notable rates of gap formation in non-hurricane years (Platt and Hermann 1986). Individual treefall gaps in these forests are often initially filled by understory species, while canopy replacement is usually accomplished by trees already present in the subcanopy. Treefall gaps have been hypothesized to maintain understory species in such forests (Peters and Platt 1996). However, the potential importance of hurricanes as disturbances that may promote the maintenance of understory species in local areas other than treerfalls directly attributed to hurricanes has not been explicity tested.

In this paper, we addressed three broad questions concerning the importance of treefall gaps in the life cycles of understory species following Hurricane Kate in Woodyard Hammock, a temperate hardwood forest located in north Florida, U.S.A. First, we examined whether recruitment of understory stems was confined to gaps in Woodyard Hammock prior to Hurricane Kate.

Next, we addressed whether post-Hurricane Kate trends in understory species recruitment were similar in local (size of a typical treefall gap) areas throughout Woodyard Hammock. Specifically, we tested whether post-hurricane recruitment differed in gaps vs. under closed canopy, and in treefall gaps with different histories based on time since gap formation (e.g., old, recent, and Kate-caused gaps). This analysis was performed on all understory species combined, as well as the two most prominent understory species in this forest, *Ostrya virginiana* (Mill.) K. Koch, *Carpinus caroliniana* Walt.; an additional analysis was performed on the remaining understory species combined. Finally, we examined whether post-Hurricane Kate survival of understory stems existing at the time of the hurricane differed in local areas throughout Woodyard Hammock. Our study enabled us to examine how understory dynamics following hurricanes may differ from those based on a gap/non-gap dichotomy.

METHODS

Study Site

Woodyard Hammock is a mixed species hardwood forest located in Leon County, Florida, USA (30°35' N, 84°20' W). This hammock is located just inland from the northern edge of Lake Iamonia, and is situated on clay-rich Miocene soils. It contains a rich assemblage of deciduous and evergreen overstory and understory plant species (Platt and Hermann 1986; Platt and Schwartz 1990), many of which are present as advance recruits of seedlings and small juveniles < 1 m tall, and do not require gaps for germination (sensu Whitmore 1989). In 1978, a 4.5 ha permanent study plot (225 x 200 m) was established in the

middle of Woodyard Hammock. Within the study plot, stems of all species ≥ 2 cm diameter at 1.5 m height (dbh) were identified (nomenclature follows Godfrey 1988), tagged, measured, and mapped. Mortality, growth, and recruitment of individual stems has been recorded in 10 biennial censuses since the establishment of the study plot.

Hurricane Kate crossed Woodyard Hammock on 21 November 1985. Hurricane force winds up to 160 km/hr were measured at a television weather tower about 10 km east of the forest, and tropical storm force winds at the study site lasted for approximately 8 hours (Batista and Platt 1997). Just prior to Kate, areas in Woodyard Hammock were characterized by three general states of forest regeneration, depending on time since last disturbance: closed canopy since 1978, maturing gaps present since 1978, and recent gaps formed since 1978. These categories, although subjective, are consistent with mature, building, and gap phases of forest regeneration (sensu Watt 1947). In addition to opening areas of closed canopy in Woodyard Hammock, Kate also directly or indirectly affected pre-existing gaps, as well as closed canopy areas by increases in light levels (Canham et al. 1991). Thus, following Kate, localized areas in Woodyard Hammock were characterized by four histories since the establishment of the study plot: closed canopy, gaps formed > 7 years before Kate, gaps formed < 7 years prior to Kate, and gaps opened directly by Kate (see Fig. 3.1). Delineation of these local histories enabled us to address specific hypotheses regarding recruitment and survival of understory species.

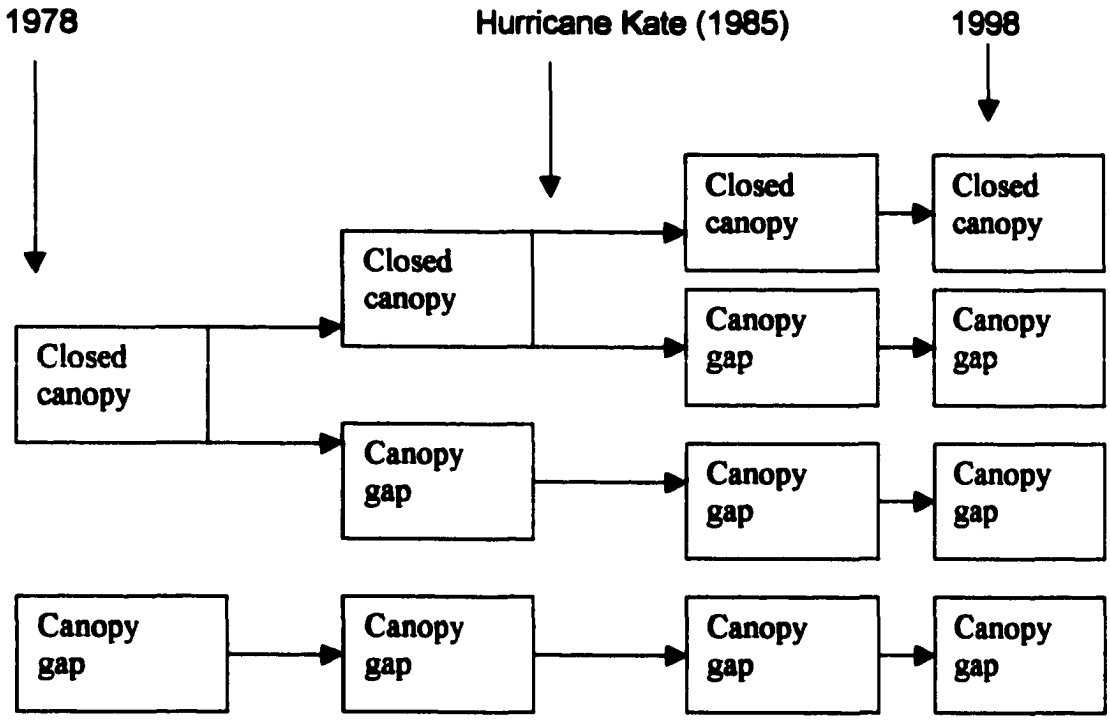

Figure 3.1. Summary of states of local areas in Woodyard Hammock since 1978. Most treefall gaps present in 1978 remained as canopy gaps through 1998. Treefall gaps formed since then either occurred prior to Hurricane Kate, or as a result of Kate.

Sampling Methods

We stratified sampling by local history within Woodyard Hammock. A total of 36 sampling plots, nine of each of the four local histories characterizing Woodyard Hammock after Kate, were selected for study. We randomly selected x and y coordinates in the mapped plot and then examined the history of each point since 1978. If the history of the general immediate area was consistent with one of the four local histories following Hurricane Kate, and that area could contain a circular plot of 10 m radius without overlapping previously selected areas, then that area was selected as a sampling plot. Plot locations were moved a few meters in any direction so that similar histories occurred within sample plots. A 10 m radius for sampling plots was chosen because it approximated the mean expanded gap (Runkle 1982) size prior to Hurricane Kate (Platt and Hermann 1986).

Data for trees recruited into each plot after 1978 were obtained from the long-term data set. We examined the number of understory trees recruited into the 2 cm dbh size class in every 2 year period from 1980-1998 and the number of understory trees that died in each 2 year period. Species designated as understory trees included *Acer rubrum*, *Aralia spinosa*, *Callicarpa americana*, *Carpinus caroliniana*, *Cercis canadensis*, *Cornus florida*, *Cornus foemina*, *Cyrilla racemifolia*, *Ilex opaca*, *Morus rubra*, *Osmanthus americana*, *Ostrya virginiana*, *Oxydendrum arboreum*, *Phytolacca americana*, *Sambucus canadensis*, and *Symplocos tinctoria*.

Analyses

We first examined whether recruitment of understory stems was confined to gaps in Woodyard Hammock prior to Hurricane Kate. More specifically, we tested whether the number of understory recruits in each of the three pre-Kate censuses was affected by the four post-Kate local histories, time, and their interaction. This approach also enabled us to verify that pre-Kate recruitment into closed canopy areas later opened by Kate was similar to that in closed canopy areas that remained under closed canopy after Kate.

We then addressed whether local histories affected post-Hurricane Kate recruitment of all understory species combined, as well as individually for *Ostrya virginiana* (hereafter *Ostrya*), *Carpinus caroliniana* (hereafter *Carpinus*), and all remaining understory species combined. Repeated measures ANOVA was used to analyze the effects of local history, time, and their interaction on the number (natural log transformed) of recruits into the 2 cm dbh size class at each biennial census following Hurricane Kate (1986 through 1998). We assumed a first-order autoregressive covariance matrix based on consistently higher Akaike's Information Criterion values among a range of potential covariance matrix options. Numbers of recruits were measured in each sampling plot such that sample plots constituted sampling error. These analyses, along with specific tests of closed canopy vs. other local site histories, were performed using the MIXED procedure in SAS.

We also addressed whether post-Kate survival through time of understory stems present at the time of Kate depended on local site history.

Proportional hazards (i.e., mortality risks) of *Ostrya* and *Carpinus* were modeled based on times (in years) until mortality. This analysis (proportional hazards modeling; Cox 1972) allows for testing whether covariates (continuous or categorical) characterizing the hazards of individuals contribute to significantly detectable differences. The underlying baseline hazard function does not matter, although the hazard function cannot be negative, and the hazards of individuals of one categorical group through time are proportional to hazards of any other group (i.e., parallel). Due to sample size limitations within sample plots, data from sample plots within treatments were pooled. These analyses, along with specific tests of closed canopy vs. gap, previous gaps vs. gaps formed by Kate, and older vs. recent pre-Kate gaps were performed using the PHREG procedure in SAS.

RESULTS

Pre-Hurricane Kate Understory Recruitment

Prior to Hurricane Kate, recruitment of all understory species combined into the 2 cm dbh size class was higher in plots in gaps than plots beneath intact closed canopy (Fig. 3.2). Repeated measures ANOVA indicated that only local history significantly affected recruitment rates (Table 3.1). Mean recruitment in plots in gaps (recent and old) were over four times higher (back-transformed) than in plots in areas under closed canopy (Fig. 3.2); this difference was significant (1 d.f. contrast, $F_{1,32} = 9.01$, $P = 0.0052$). Recruitment in plots with gap histories prior to Hurricane Kate were similar (1 d.f. contrast, $F_{1,32} = 1.18$, $P = 0.2854$), and recruitment in plots under closed canopy were

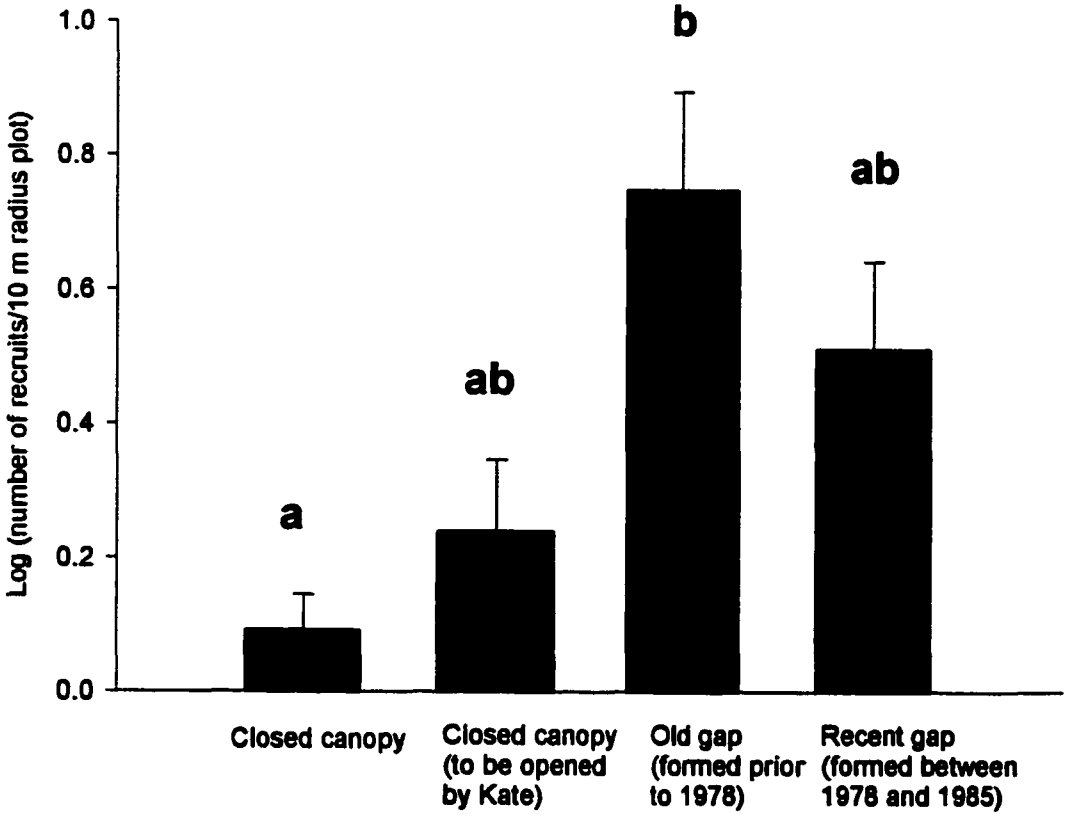

Figure 3.2. Recruitment rates (back-transformed) of understory stems (all understory species) per 10 m radius plot prior to Hurricane Kate as a function of local plot history. Local plot histories include those that have remained under closed canopy since 1978, those previously under closed canopy but opened by Kate, those in gaps formed > 7 years prior to Kate, and those in gaps formed < 7 years prior to Kate. Data are displayed as means (pooled across years) ± SE. Histories with different letters are significantly different ($P < 0.05$) based on adjusted Tukey pairwise comparisons.

Table 3.1. Analysis of variance table for effects of plot history, time, and their interaction on recruitment rates (numbers of stems [natural log transformed] recruited into the 2 cm dbh size class per 2 year period per 10 m radius plot) of all understory stems prior to Hurricane Kate. Plot history refers to post-Hurricane Kate designations (refer to text); thus two local plot histories are under closed canopy in this analysis.

Source	NDF	DDF	Type III F	Pr > F
History	3	32	3.55	0.0252
Time	2	32	0.27	0.7678
History x Time	6	32	2.10	0.0811

also similar (1 d.f. contrast, $F_{1,32} = 0.46$, $P = 0.5043$). These results indicate the importance of treefall gaps, and that the two types of closed canopy areas prior to Hurricane Kate (one of which was opened up by Kate, while the other remained closed canopy after Kate) did not differ with respect to understory recruitment dynamics.

Post-Hurricane Kate Understory Recruitment

Following Hurricane Kate, understory species recruitment was lowest in areas under closed canopy, and higher in gaps of all types (Fig. 3.3). Local history significantly affected understory recruitment (Table 3.2), and in particular, local areas in gaps of all types had significantly higher recruitment than in areas under closed canopy (Tukey comparison of means; $P < 0.01$). There were no differences in recruitment in gaps of all types; hence removal of the canopy stratum was not necessary for understory recruitment following Hurricane Kate. Understory recruitment was also significantly affected by time (Table 3.2). Pairwise comparison of means indicated that years of highest (1994) and lowest (1988) recruitment significantly differed across all local areas (Tukey-Kramer pairwise comparisons; $P = 0.0386$). The number of understory recruits was not significantly influenced by the interaction of local history and time (Table 3.2).

Post-Hurricane Kate recruitment patterns of *Ostrya*, *Carpinus*, and other species were also affected by local history and time, but each in slightly different ways. The number of *Ostrya* recruits was higher in gaps of all types, and appeared to reach a maximum in 1992 (Fig. 3.4). *Ostrya* recruitment was

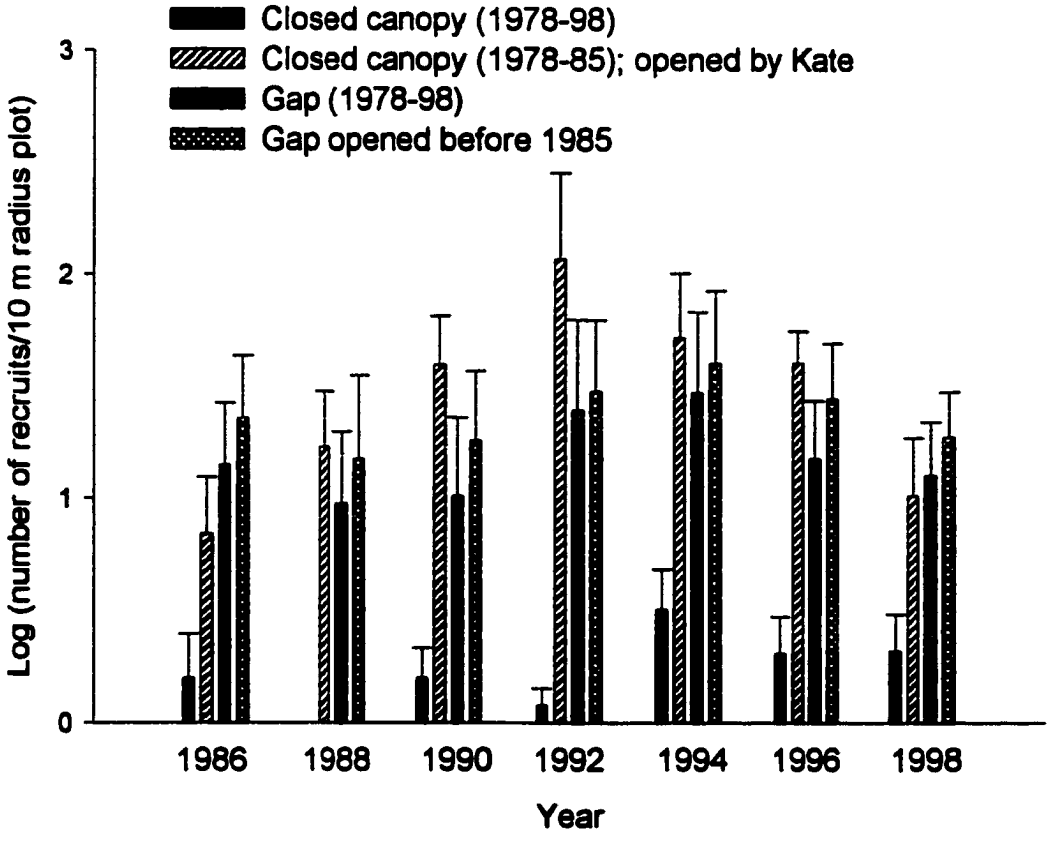

Figure 3.3. Mean number of all understory recruits (back transformed ± SE) per 10 m radius plot counted at each post-Hurricane Kate census.

Table 3.2. Analysis of variance table for effects of local history, time, and their interaction on recruitment rates (numbers of stems [natural log transformed] recruited into the 2 cm dbh size class per 2 year period per 10 m radius plot) of all understory stems following Hurricane Kate.

Source	NDF	DDF	Type III F	Pr > F
History	3	32	9.34	0.0001
Time	6	192	2.55	0.0214
History x Time	18	192	1.30	0.1931

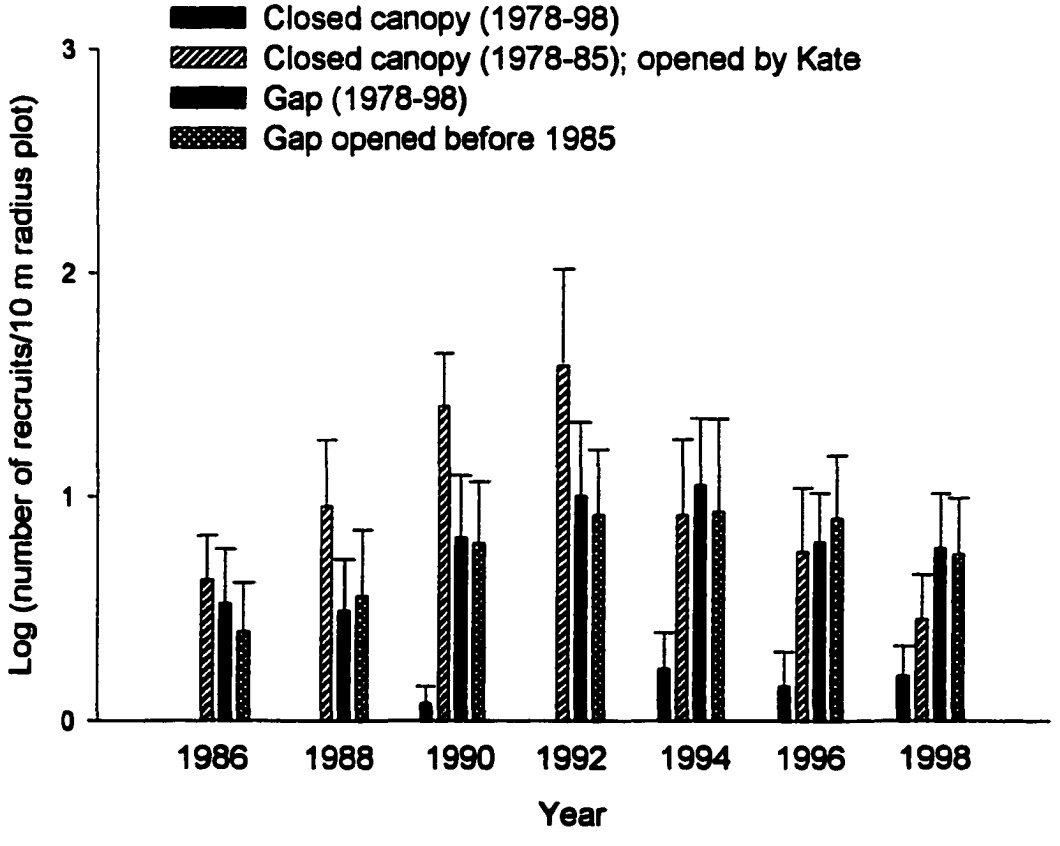

Figure 3.4. Mean number of *Ostrya virginiana* recruits (back transformed ± SE) per 10 m radius plot counted at each post-Hurricane Kate census.

significantly affected by local history and time, but no interaction was evident (Table 3.3). Recruitment was higher in local areas in gaps of all types than under closed canopy (Tukey comparison of means; $P < 0.05$), and was significantly higher in 1990 and 1992 than in 1986 (Tukey-Kramer pairwise comparisons; $P < 0.05$). Post-hurricane recruitment for *Carpinus* did not increase until 1992, and the increase was primarily confined to gaps (Fig. 3.5). *Carpinus* recruitment was significantly affected by local history and time, but not by their interaction (Table 3.4). Recruitment was significantly higher in local areas in gaps formed by Kate and gaps formed just prior to Kate than under closed canopy (Tukey comparison of means; $P < 0.05$), and recruitment throughout Woodyard Hammock was significantly higher in 1992, 1994, and 1996 than in the three censuses following Kate (Tukey-Kramer pairwise comparisons; $P < 0.05$). Post-Kate recruitment of all other understory species combined was less affected by local history and time than *Ostrya* and *Carpinus* (Fig. 3.6). Recruitment of other understory species was only marginally affected by local history, and significantly differed among times (Table 3.5).

Post-Hurricane Kate Stem Survival

Post-Hurricane Kate mortality risk of *Ostrya* stems existing at the time of the hurricane was marginally affected by previous local site history (Wald $\chi^2_3 = 6.8148$, $P = 0.0780$). The highest risk of mortality after Kate occurred in plots that were beneath closed canopy before Kate and remained beneath closed canopy, and in plots where the canopy was opened by Kate that were previously beneath closed canopy (no significant difference between these two

Table 3.3. Analysis of variance table for effects of plot history, time, and their interaction on recruitment rates (numbers of stems [natural log transformed] recruited into the 2 cm dbh size class per 2 year period per 10 m radius plot) of *Ostrya virginiana* stems following Hurricane Kate.

Source	NDF	DDF	Type III F	Pr > F
History	3	32	4.93	0.0063
Time	6	192	2.51	0.0234
History x Time	18	192	1.10	0.3542

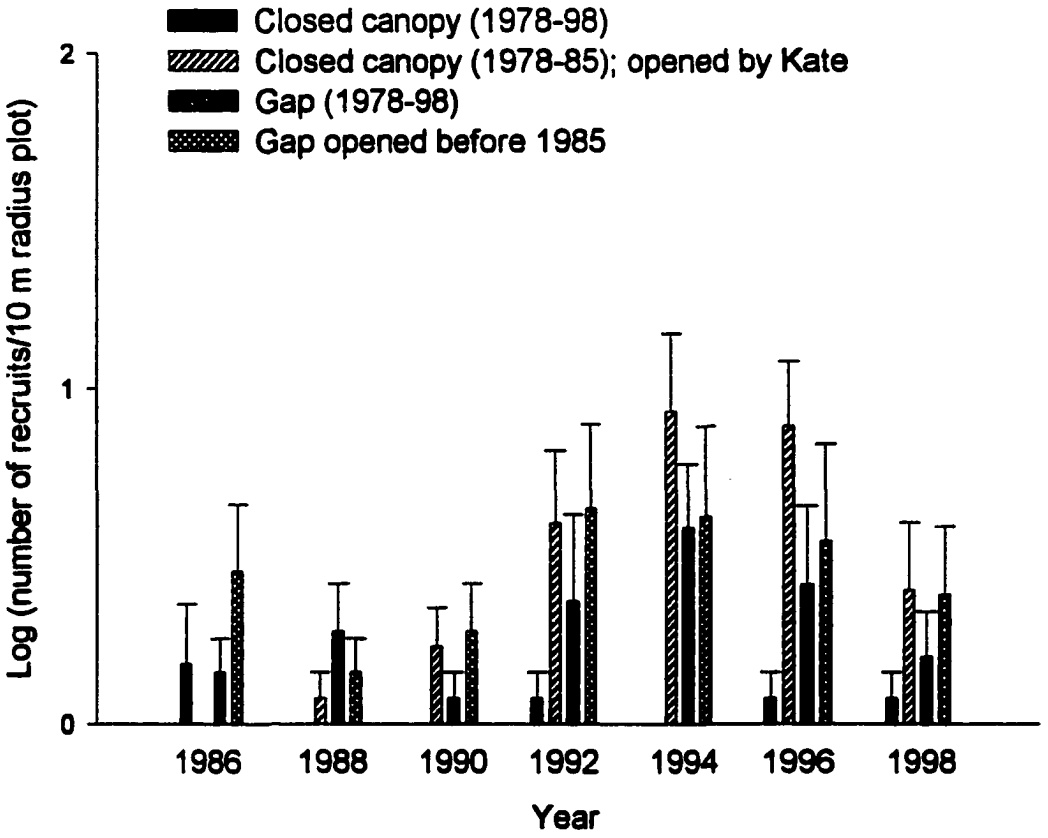

Figure 3.5. Mean number of *Carpinus caroliniana* recruits (back transformed ± SE) per 10 m radius plot counted at each post-Hurricane Kate census.

Table 3.4. Analysis of variance table for effects of plot history, time, and their interaction on recruitment rates (numbers of stems [natural log transformed] recruited into the 2 cm dbh size class per 2 year period per 10 m radius plot) of *Carpinus caroliniana* stems following Hurricane Kate.

Source	NDF	DDF	Type III F	Pr > F
History	3	32	3.10	0.0406
Time	6	192	3.97	0.0009
History x Time	18	192	1.28	0.2054

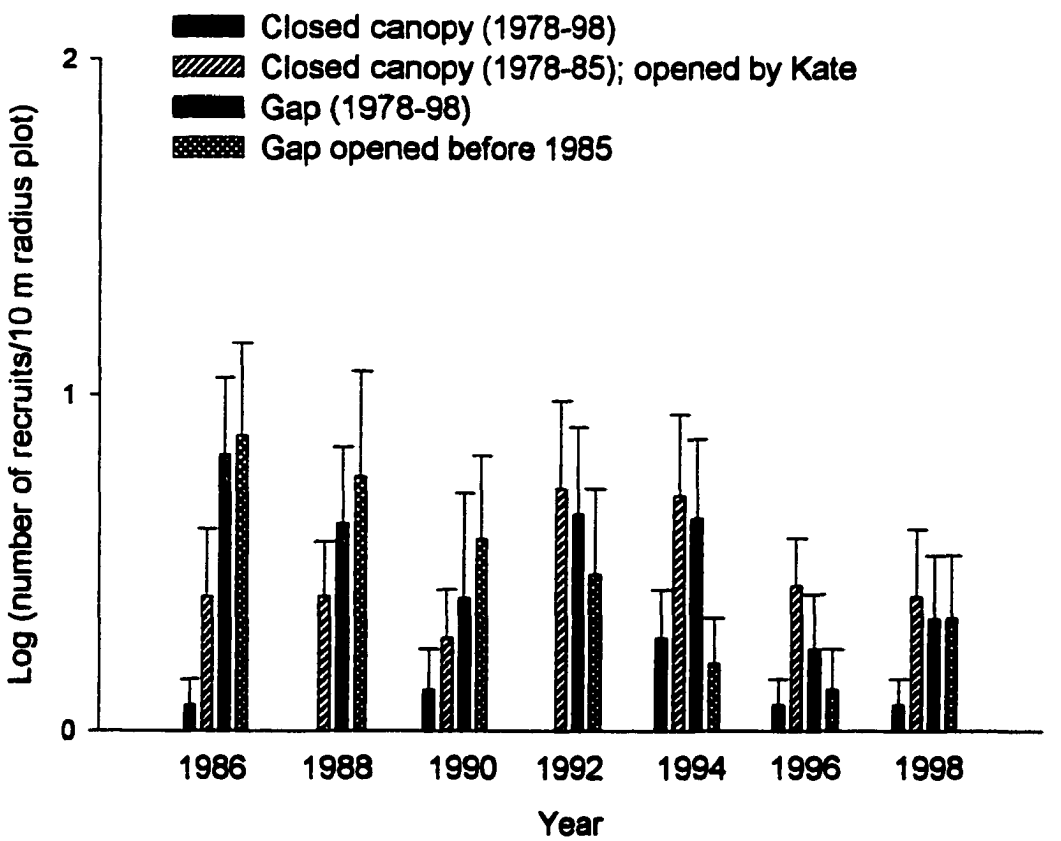

Figure 3.6. Mean number of understory recruits excluding *Ostrya virginiana* and *Carpinus caroliniana* (back transformed ± SE) per 10 m radius plot counted at each post-Hurricane Kate census.

Table 3.5. Analysis of variance table for effects of plot history, time, and their interaction on recruitment rates (numbers of stems [natural log transformed] recruited into the 2 cm dbh size class per 2 year period per 10 m radius plot) of all understory stems excluding *Ostrya virginiana* and *Carpinus caroliniana* following Hurricane Kate.

Source	NDF	DDF	Type III F	Pr > F
History	3	32	2.32	0.0941
Time	6	192	2.23	0.0421
History x Time	18	192	1.15	0.3078

treatments; Wald χ_1^2 = 0.0502, P = 0.8227). Stems that were in recent and maturing gaps at the time of Kate had lower mortality risks than those in areas with the aforementioned local site histories. However, the only significant difference was between stems in gaps formed just prior to Kate compared with gaps formed by Kate (pairwise comparison; Wald χ_1^2 = 4.5056, P = 0.0338).

Post-Hurricane Kate mortality risk of *Carpinus* stems existing at the time of Kate was significantly affected by local site histories (Wald χ_3^2 = 14.3862, P = 0.0024). Post-Kate mortality in certain types of gaps was significantly different than in plots in areas that have been under closed canopy throughout. Mortality risk was higher in gaps formed by Kate and in old gaps than in areas under closed canopy (pairwise comparisons; Wald χ_1^2 = 6.1314, P = 0.0133, and Wald χ_1^2 = 6.2162, P = 0.0127, respectively). In addition, post-Kate mortality risk for *Carpinus* in gaps formed prior to Kate was higher in older than more recent gaps (Wald χ_1^2 = 8.2627, P = 0.0040).

Discussion

Hurricanes are disturbances that open space and influence a variety of areas within forests upon impact. These large-scale disturbances thus produce a wider range of patch types than predicted using a gap/non-gap dichotomy. By affecting areas of forests at different stages of small, localized gap phase dynamics, hurricanes may have a profound effect on understory dynamics. In our study, recruitment of understory stems following Hurricane Kate occurred in all areas of Woodyard Hammock except for those under closed canopy. In addition, similar amounts of recruitment occurred in previously formed gaps as

occurred in overstory gaps formed by the hurricane. Canopy gaps formed by the hurricane, therefore, were not necessary for understory recruitment. Thus, at the scale of forest stands, hurricanes may have a much broader impact on recruitment than single treefall gaps by themselves. This may be possible due to the large area of canopy gaps created by hurricanes and the subsequent ability for light to reach adjacent and nearby areas of the understory statum (particularly in temperate forests; see Poulson and Platt 1990, Canham et al. 1991).

Seedling banks of understory stems appear to be long-lived in Woodyard Hammock. Pre-Hurricane Kate recruitment of understory stems in areas of gaps formed between 1978 and 1985, and even in older gaps formed prior to 1978, was dominated by *Ostrya* and *Carpinus*. Following Hurricane Kate, *Ostrya* and *Carpinus* were once again the most common understory recruits in newly formed gaps, as well as in pre-existing gaps that already had larger *Ostrya* and *Carpinus* stems. This suggests that a persistent *Ostrya* and *Carpinus* seedling bank capable of existing under closed canopy was present in Woodyard Hammock from before the establishment of the study plot (1978) through the time of Hurricane Kate (1985). Similar patterns for overstory trees with seedling or sapling banks in closed canopy forests have been shown (Grime 1979, Silvertown 1982, Clark and Clark 1992, Clark et al. 1993, Marks and Gardescu 1998), but have not been well documented for understory species.

Recent local histories of small areas within forests may affect post-hurricane survival of understory species. For both *Ostrya* and *Carpinus*, post-Kate survival of stems existing at the time of the hurricane was highest in areas in gaps opened just prior to Kate. This may have been due to increased light levels from new, nearby canopy gaps and/or decreased risk of damage from the lack of overtopping canopy trees. Such areas of forests may therefore be most beneficial to understory species for two reasons; not only is recruitment possible in such gaps, but survival of pre-existing stems is high as well. This may allow certain understory species to survive longer as reproductive individuals, and hence be less fugitive (see Peters and Platt 1996), in certain areas of forests. Post-hurricane survival of pre-existing *Ostrya* and *Carpinus* stems was lowest in areas in canopy gaps opened by Kate. This may have been due to increased damage risk and subsequent mortality from falling canopy trees. This finding is also consistent with a model in which hazards of stems can only be decreased if a disturbance occurs while a gap is still closing, and that at some point after closure, suppression and/or senescence does not allow for a positive survival response to gap formation.

Population models of understory species in hurricane-impacted forests may benefit from knowledge of both pre- and post-hurricane local site conditions that can only be gained from long-term studies. This approach may be more useful than predictions based on a gap/non-gap dichotomy. The latter framework would have predicted no post-hurricane understory recruitment in pre-existing, unclosed, canopy gaps; recruitment would have only taken place

at the time of the original canopy gap formation. In addition, the time an individual stem remains reproductively mature (i.e., > 2 cm dbh) may depend on its past history at the time of the next disturbance. Our results are consistent with the hypothesis that Hurricane Kate caused decreased hazards of *Ostrya* and *Carpinus* stems in recent gaps that were not closed at the time of Kate. Growth of advance recruits may also be governed by such a relationship (but see Marks and Gardescu 1998).

Based on our results, we can develop predictions for understory species dynamics following the next hurricane. Such localized predictions would not be possible solely with information on the time since the last hurricane (as Peterson and Carson 1996). As the interval between hurricanes increases, the presence of advance recruits throughout the forest would likely decrease through time. Thus, provided the next hurricane occurred before stores of advance recruits were depleted, we would predict that *Ostrya* and *Carpinus* would quickly dominate the understory recruits into the 2 cm dbh size class in Woodyard Hammock, provided that the hurricane opened a substantial portion of the canopy, and that a modest portion of the forest contained local areas of recent and older gaps. Based on our recruitment data, this pattern may be more evident in *Ostrya* than *Carpinus*.

GENERAL SUMMARY

Understory trees of warm temperate mixed species hardwood forests of northern Florida (USA) are influenced by a number of environmental and ecological factors. The habitat where *Taxus floridana* occurs on north-facing ravine midslopes is unique. North-facing midslopes with *T. floridana* had higher densities of American beech (*Fagus grandifolia*) and southern magnolia (*Magnolia grandiflora*) than randomly chosen north-facing midslopes. These species are thought to have been more widespread in the Apalachicola River Bluffs region prior to European settlement (Delcourt and Delcourt 1977), suggesting that habitat favorable to *T. floridana* has been altered over the past two centuries. North-facing midslopes with *T. floridana* also contained higher densities of other evergreen understory species such as *Ilex coriacea*, *Ilex opaca*, and *Kalmia latifolia*, than randomly chosen north-facing midslopes. This suggested that *T. floridana* may be confined to local areas in ravines that are also primarily suitable to evergreen understory trees.

The present demography of *T. floridana* populations throughout its range was predicted to be insufficient for future long-term persistence. Even a ten-fold increase in seedling recruitment in 1996 noted throughout its range had little effect on long-term population growth rates. This finding suggests that its continued persistence in the areas where it exists may depend on demographic changes in other portions of its life cycle besides seedling recruitment. Long-term persistence will undoubtedly depend on continued high survival of large reproductive adults; this would cause population declines to be slow. However,

long-term persistence may also depend on disturbances such as hurricanes or slope slumping that promote asexual reproduction through the layering of stems, which in turn assists in bypassing the seedling bottleneck. In this scenario, increasing juvenile (i.e., small stem) survival may improve the likelihood of long-term persistence despite their relatively small contribution to long-term population growth rates.

The demography of understory trees in gaps following hurricanes in Woodyard Hammock was consistent with their being dependent on prior gap history. Recruitment in gaps following Hurricane Kate was similar in gaps of different ages for all understory trees combined, as well as for *Ostrya virginiana* and *Carpinus caroliniana*, the two most abundant understory trees in the forest. Thus, the hurricane may have increased light levels everywhere in Woodyard Hammock except for local areas that remained under closed canopy. Prior gap history (i.e., gap age) in local areas did affect mortality risk of pre-existing stems following Hurricane Kate. Thus, following a hurricane, the dynamics of understory trees may be a function of the gap-phase state of local areas within the forest. If, for example, a hurricane impacts a forest characterized by a moderate aerial coverage of previously formed gaps (e.g., short interval between hurricanes, or high rate of background gap formation), the demographic responses of understory trees may be much different than if the forest is characterized by few treefall gaps (e.g., long interval between hurricanes). Thus, predictions made based solely on a gap/non-gap dichotomy

may not be entirely useful in mixed species hardwood forests of the southeastern United States.

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APPENDIX: LETTER OF PERMISSION

March 1, 2000

Dr. Beverly Collins
Editor-in-Chief
Journal of the Torrey Botanical Society
Savannah River Ecology Laboratory
P.O. Drawer E
Aiken, South Carolina 29802

Dear Dr. Collins:

I am writing to obtain permission to reproduce text and data from the following article in my dissertation:

> Kwit, C., M. W. Schwartz, W. J. Platt, and J. P. Geaghan. 1998. The distribution of tree species in steepheads of the Apalachicola River Bluffs, Florida. Journal of the Torrey Botanical Society 125 (4): 309-318.

I am currently a candidate for the Ph.D. degree in the Department of Biological Sciences at Louisiana State University. I will be graduating in August of this year, so permission needs to be granted by the end of May at the latest.

Thank you very much for your assistance.

Sincerely,

Charles Kwit

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30 April, 2000

Charles Kwit
Department of Biological Sciences
Louisiana State University
508 Life Sciences building
Baton Rouge, Louisiana 70803-1715

Dear Dr. Kwit:

Our goal at the **Journal of the Torrey Botanical Society** is to propagate information about the biology of plants. We are always pleased when something we have published is worthy of use in education or research. Therefore, we are pleased to give permission for you to reproduce text and data from Kwit, C., M. W. Schwartz, W. J. Platt, and J. P Geaghan. 1998. The distribution of tree species in steepheads of the Apalachicola River Bluffs, Florida. J. Torrey Bot. Soc. 125(4):309-318.

Sincerely yours,

Beverly Collins
Editor-in-Chief

VITA

Charles Kwit was born June 11, 1970, in Maywood, Illinois. He grew up in Glen Ellyn, Illinois, and graduated from Benet Academy in Lisle, Illinois, in 1988. He entered the College of DuPage in Glen Ellyn, Illinois, in 1988, and received an associate of science degree in 1990. He entered the University of Wisconsin-Madison in 1990 and received a bachelor of science degree in wildlife ecology in 1992. While at the University of Wisconsin, he was employed by the Department of Botany and worked on projects concerning the distribution of aquatic macrophytes in northern Wisconsin under the direction of Dr. Thomas Givnish. He also worked at the Morton Arboretum in Lisle, Illinois, on songbird nesting ecology in oak woodlands under the direction of Dr. Christopher Whelan. In fall of 1993, he entered the Department of Botany at Louisiana State University and began his doctoral work under the direction of Dr. William Platt. He will receive the degree of Doctor of Philosophy in August, 2000.

DOCTORAL EXAMINATION AND DISSERTATION REPORT

Candidate: Charles Kwit

Major Field: Plant Biology

Title of Dissertation: Habitat and Demography of Understory Trees in Mixed Species Hardwood Forests of Northern Florida, USA

Approved:

William J Platt
Major Professor and Chairman

Dean of the Graduate School

EXAMINING COMMITTEE:

Stanley B. Carpenter

James D. Gleaghan

Carol C. Horvitz

Julie S. Denslow

Date of Examination:

17 April 2000